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SYSTEMATICS OF THE OMOMYIDAE (TARSIIFORMES, PRIMATES) TAXONOMY, PHYLOGENY, AND ADAPTATIONS

FREDERICK SIGMOND SZALAY

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SYSTEMATICS OF THE OMOMYIDAE (TARSIIFORMES PRIMATES) TAXONOMY, PHYLOGENY AND ADAPTATIONS

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ABSTRACT

The taxonomy and analyses of the phylogenetic relationships and adaptations of the subfamilies Anaptomorphinae, Omomyinae, and Ekgmowechashalinae of the undoubted tarsiiform family Omomyidae are presented. The exclusively European subfamily Microchoerinae, although best referred to the Omomyidae, is not revised; pertinent information is treated in the study of phylogenetic ties of the family. The Omomyidae, as far as is known, is Holarctic in distribution. The known stratigraphic ranges are: Anaptomorphinae, early to medial Eocene (North America and Europe); Omomyinae, early Eocene to early Oligocene (North America; early Eocene in Asia); Ekgmowechashalinae, late Oligocene (North America); Microchoerinae, medial Eocene to early Oligocene (Europe).

Character analysis of the primarily dental, cranial, and postcranial evidence is presented. Several derived character states, particularly the relative size and point of entry of the intrabullar carotid circulation, unequivocally tie the Omomyidae to the Tarsiidae and also to the Platyrrhini and Catarrhini, thus helping to substantiate the monophyletic status of the suborder Haplorhini, as contrasted with the suborder Strepsirhini. The origin of the Omomyidae, the most primitive known family of the Tarsiiformes, was probably from a primitive lemuriform primate that most closely resembled a member of the Eocene Adapidae.

The classification presented is a compromise based on morphological diversity and phylogeny, but it is consistent with the inferred phylogeny.

Family Omomyidae
- Subfamily Anaptomorphinae
  - Tribe Anaptomorphini
    - Subtribe Teilhardinina
      - *Teilhardina*
      - *Chlororhysis*
    - Subtribe Anaptomorphina
      - *Anaptomorphus*
    - Subtribe Tetoniina
      - *Tetonius*
      - *Anemorhysis*
      - *Absarokius*
      - *Mckennamorphus*, new genus
  - Tribe Trogolemurini, new
    - *Trogolemur*
- Subfamily Omomyinae
  - Tribe Omomyini
    - Subtribe Omomyina
      - *Omomys*
      - *Chumashius*
    - Subtribe Mytoniina, new rank
      - *Ourayia*
      - *Macrotarsius*
  - Tribe Washakiini, new
    - *Loveina*
    - *Shoshonius*
    - *Washakius*
    - *Dyseolemur*
    - *Hemiacodon*
  - Tribe Uintaniini, new
    - *Uintanius*
  - Tribe Utahiini, new
    - *Utahia*
    - *Stockia*
  - Tribe Rooneyiini, new
    - *Rooneyia*
- Subfamily Ekgmowechashalinae, new
  - *Ekgmowechashala*

Family and suborder uncertain
- *Donrussellia*, new genus

RESUME

Dans cet article nous présentons la taxonomie et l'analyse des relations phylogenetiques et des adaptations des sousfamilles Anaptomorphinae, Omomyinae, et Ekgmowechashalinae appartenants a la famille des Omomyidae. La position des Microchoerinae, qui sont considérés comme faisant partie des Omomyidae, n'est past revisée malgré que les sources d'information ayants a faire avec le problem des relations phylogénetiques de cette famille, sous analysees. Autant que nous le sachons les Omomyidae proviennent d'Amerique du Nord et d'Europe. Les variations statigraphiques connues a present sont les suivantes: Anaptomorphinae, de l'Eocène inférieur jusqu'au l'Eocène moyen (Amerique du Nord et l'Europe); Omomyinae, de l'Eocène inférieur jusqu'à l'Oligocène inférieur (Amerique du Nord; Asie, l'Eocène inférieur); Ekgmowechashalinae,

Oligocène supérieur (Amerique du Nord); Microchorinae, de l'Eocène moyen jusqu'a l'Oligocène (Europe).

Dans ce travail nous présentons l'information dentaire, crânienne, et post-crânienne. Plusieurs caractères derivés, particulierement la largeur relative et le point d'entré de la circulation carotide intrabullaire établissent une relation entre les Omomyidae et les Tarsiidae aussi bien qu'avec les Platyrrhini et Catarrhini. Ainsi ils contribuent a la confirmation du status monophyletique du sousordre des Haplorhini en les comparant sousordre aux Strepsirhini. Les Omomyidae, la famille la plus primitive des Tarsiiformes, sont probablement derivés d'un group de primates lemuriformes primitives, un taxon qui resemble le plus etroitement un des Adapidae de l'Eocène.

La classification presentée dans le resumé anglais represents un compromis base sur la diversité morphologique et la phylogénie, mais aussi consistant avec la phylogénie.

ZUSAMMENFASSUNG

Die Taxonomie and Analyse der phylogenetischen Beziehungen und Anpassungen der Subfamilien der Anaptomorphinae, Omomyinae, und Ekgmowechashalinae, die zweifellos zu der tarsiiformen Familie der Omomyidae gehören, wurde dargestellt. Die ausschlieslich Europaische Familie der Microchoerinae, die am besten den Omomyidae zugewiesen wird, wurde nicht revidiert, aber die pertinente Information wurde in der Analyse der phylogenetischen Beziehungen dieser Familie behandelt. Soweit wir wissen, sind die Omomyidae von Nord Amerikanischem und Europaischem Ursprung. Die stratigraphischen Bedingungen sind wie folgt: Anaptomorphinae, Früh bis Mittel Eocene (Nord Amerika und Europa); Omomyinae, Frühes Eocene bis Frühes Oligocene (Nord Amerika; Asie, Frühes Eocene); Ekgmowechashalinae, Frühes Oligocene (Nord Amerika); Microchoerinae, Mittel Eocene bis Oligocene (Europa).

In der vorliegenden Arbeit wurde eine Analyse der Zähne, der craniellen und der post-craniellen Daten ausgeführt. Einige abgeleitete Charakterzüge, besonders die relative Grösse und der Eintrittspunkt der intra-bullaren karotiden Zirkulation, bringen die Omomyidae in zweifellosen Zusammenhang mit den Tarsiidae, den Platyrrhini und Catarrhini. Diese Tatsache trägt dazu bei die morphyletische Stellung der Unterordunug der Haplorhini im Gegensatz zu den Strepsirhini zu sichern. Die Omomyidae, die die primitievste Familie der Tarsiiformen dorstellt, stammen wahrscheinlich von primitiven lemuriformen Primaten ab, die am meisten dem Morphotype der Eocenen Adapiden ähneln.

Die Kassifikation, die in der Englischen Zusammenfassung gegeben wurde, stellt einen Kompromis dar begründet auf morphologische Verschiedenheit und Entwicklungsgeschichte, und ist nicht im Widerspruch zu der indirekt gefolgerten Entwicklungsgeschichte.

INTRODUCTION

I dedicate this work to the memory of William King Gregory—extraordinary student and monographer of fossil vertebrates.

My aim in this monograph is primarily threefold. First, to sort out valid from invalid species. Second, to review the comparative morphological evidence of the dentition and the rest of the cranium to trace the phyletic interrelationships of omomyid primates and the affinities of the family to other primates. I have also attempted to balance classification above the species level within the family. Third, to present some preliminary analyses of omomyid adaptations with emphasis on the dentition.

If there is value to a monograph, it should be in proportion to the degree to which it has achieved synthesis, to its reliability, and its power to stimulate other scientists. Frequently, however, conclusions go astray, relevant evidence is sometimes overlooked, and, therefore, along with new understanding from related fields, reinterpretation of timeless evidence of fossils and the living forms is periodically necessary. To fulfill the goals of reference and reliability it is of utmost significance that the most important part of the evidence be presented in an unbiased manner. Although the various composite drawings are biased both by the views of the artist and of the author for whom they were prepared, the accompanying stereophotographs should balance the scale. Interpretations do not have to be accepted on face value: some of the evidence presented on stereophotographs should encourage critical review by other students.

While this work was in preparation and in press numerous important specimens of known taxa and new species and genera were discovered, probably altering some of the conclusions. Added to this, the mounting interest in the evolutionary history of the primates heightens the meaning of the adage that each worthwhile work carries seeds of its own obsolescence.

This monograph is far from definitive, not only because it deals with a mere fraction of the actual omomyid radiation, which is continually being discovered, but because it does not attempt to give fully satisfactory answers to some of the most important problems surrounding these species. For example, no detailed functional studies are made to determine feeding preferences of the species studied. Causal knowledge of living primates and other mammalian dentitions is still in its infancy, despite the major studies that have been started by a large number of workers toward an understanding of the mechanical problems of mastication and their biological roles. For a work to be called definitive on any one of the extinct species, paleontologists must be able to 1) explain why teeth and bones have their particular form, taking their explanations from phylogeny, mechanics, and statics, and 2) cogently argue for a particular taxon having a particular locomotor behavior and feeding preference and also a specific kind of population dynamics, in addition to presenting zoogeographic and genealogical data that can sometimes be grasped from a single specimen.

Descriptive statements of dental morphology, although necessary for taxonomy, tell little of the mechanical function or the associated biological role of those structures in a particular taxon. One hopes, however, that the day will come when descriptions of dental remains will carry within them statements of meaning about their mechanical function and perhaps even their biological roles. The beginnings of a major step have been taken by Every (1972), yet historically entrenched nomenclature and lack of accepted, widely understood, and extensively used terminology forces the use of the tooth nomenclature of Cope-Osborn (for nomenclature see especially Van Valen, 1966, and Szalay, 1969a). The discussions below use, *faute de mieux*, this poorly suited language of taxonomic dental descriptions.

Contrary to a usual practice in morphological monographs, in this work descriptive sections are kept to a minimum. The pertinent points are emphasized in the discussions and the assessment of adaptations are supported by the illustrations.

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All the drawn figures (except figs. 126 and 127, which were prepared by Ms. Biruta Ackerbergs) were executed by Ms. Anita J. Cleary. Without her patient talents the art work of this study would not have been possible. Ms. Miriam Siroky, in her capacity as scientific assistant, was immeasurably helpful during the final year of preparation of the plates and the manuscript.

ABBREVIATIONS

The following are used for collections of fossils and for metrical parameters of specimens.

Institutions

AC, Amherst College Museum, Amherst College
AMNH, the American Museum of Natural History, Department of Vertebrate Paleontology
AMNH (DM), the American Museum of Natural History, Department of Mammalogy
ANS, Academy of Natural Sciences
CM, Carnegie Museum
FM, Field Museum of Natural History
IRSNB, Institut Royal des Sciences Naturelles de Belgique
KNM, Kenya National Museum
LACM, Los Angeles County Museum
MCZ, Museum of Comparative Zoology, Harvard University
MNHN, Muséum National d'Histoire Naturelle
PU, Princeton University
SDSM, South Dakota School of Mines, Rapid City
UCM, University of Colorado Museum
UCMP, University of California Museum of Paleontology, Berkeley
USNM, National Museum of Natural History, Smithsonian Institution
UT, University of Texas
UW, University of Wyoming
YPM, Yale Peabody Museum

Measurements

AW, anterior width (greatest width of trigonid)
CV, coefficient of variation
KS, kurtosis
L, length
M, mean
N, number
OR, observed range
PW, posterior width (greatest width of talonid)
R, coefficient of correlation
SD, standard deviation
SE, standard error
SK, skewness
W, width

Anatomical Terms Used for the Basicranium

APA, ascending pharyngeal artery
ACF, anterior carotid foramen
AM, annulus membrane
AS, alisphenoid
B, bulla
BO, basioccipital
BS, basisphenoid
CF, carotid foramen
CNJ, canal for nerve of Jacobson
COF, condyloid foramen
ECA, external carotid artery
EF, eustachian foramen
EJV, external jugular vein
ENJ, exit for nerve of Jacobson
ENT, entotympanic
EO, exoccipital
ER, epitympanic recess
FC, facial canal
FEO, fenestra ovale
FER, fenestra rotunda
FLA, foramen lacerum anterior
FLP, foramen lacerum posterior
FM, foramen magnum
FNJ, foramen for nerve of Jacobson
FOO, foramen ovale
FSRS, foramen for superior ramus of stapedial artery
GF, glenoid fossa
ICA, internal carotid artery
IJV, internal jugular vein
IPS, inferior petrous sinus
IPSF, inferior petrous sinus foramen
IRSA, inferior ramus of stapedial artery
JS, jugular spine
LCA, lateral carotid artery
LCAC, lateral carotid arterial canal
MP, mastoid process
OAM, ossified annulus membrane
P, petrosal
PA, promontory artery
PC, promontory canal
PF, promontory foramen (=foramen lacerum medium)
PGF, postglenoid foramen
PGP, postglenoid process
PM, petromastoid
PR, promontorium of petrosal
SA, stapedial artery
SBP, superior border of the petrosal
SC, stapedial canal
SF, styloid fossa
SMF, stylomastoid foramen
SOAM, support for ossified annulus membrane
SQ, squamosal
TH, attachment for hyoid arch
TP, tympanic process
VF, vidian foramen

HISTORY OF INVESTIGATIONS

I make no attempt here to review the history of discovery, descriptions, and taxonomy of all relevant primates. All early Tertiary primates are pertinent to the various concepts of the taxonomic names related to the Omomyidae, beginning with the early nineteenth-century description of the first of the fossil primates, that of *Adapis parisiensis* by Cuvier. The taxonomic status of many fossil primates has fluctuated and will continue to do so. A thorough, relevant review can be found in Gregory (1920, pp. 55-62), which is the most detailed source on early Tertiary primate systematics up to its time with an emphasis on the Eocene lemuriforms.

The original concept of the Omomyidae dates back to Trouessart, 1879, who used the term Omomynae based on *Omomys* Leidy, 1869. The Anaptomorphidae as a family group name was first used by Cope in 1883, and the concept of the Microchoeridae was created by Lydekker in 1887. The name Pseudolorisinae was first used by Simpson in 1940. Although a great deal of fluctuation followed in the allocation of various genera to the Anaptomorphidae, most North American and many European genera were customarily referred to this group, allocated to one of several then recognized subfamilies.

Cope's (1883) Anaptomorphidae, a concept at its inception based primarily on the skull of *Tetonius homunculus* (= "*Anaptomorphus*" *homunculus*), signified that this family was early recognized as distinct from the Adapidae, the latter already well known from skulls. Another important step was the consolidation of the then known genera in Schlosser's (1887) notes pointing to special similarities between the North American *Omomys* and the European *Necrolemur*.

Wortman (1903), in his important monograph on Eocene primates presented a major review of primate phylogeny and classification. Unlike most of his predecessors, Wortman boldly asserted the closer ties of *Tarsius* and allies to the platyrrhines and catarrhines than to lemuroids, using the suborder Anthropoidea, a concept originally intended for platyrrhines and catarrhines only, for the three former groups. Within the tarsioid primates, which he referred to as Paleopithecini, Wortman recognized the Tarsiidae and the Anaptomorphidae. Astutely, he divided the Anaptomorphidae into the Omomyinae and Anaptomorphinae, in which he included *Microchoerus* and *Necrolemur*. Years later a new higher category erected by Gregory (1915), the Tarsiiformes, included two families, the Microchoeridae and the Tarsiidae. The Tarsiidae encompassed both the Anaptomorphinae and Omomyinae of Wortman. Gregory's Tarsiiformes was of equal rank to the Lemuriformes and Lorisiformes within the suborder Lemuroidea. Consequently in his monograph on *Notharctus* Gregory (1920) clearly indicated his allocation of the Anaptomorphidae when he referred to skulls of *Tetonius* and *Necrolemur* as those of tarsiiforms.

Simpson in his 1937 milestone of a faunal study of the Paleocene Fort Union of Crazy Mountain Field in the section on primates referred to the Eocene nonlemuroids as "acknowledged tarsioids" (p. 145), and considered the Paleocene genera, grouped under the Paromomyidae, as having tarsioid ties. He later carried this suggestion further (see below) by including the Paromomyinae in the Anaptomorphidae. Later still, in his 1940 study of skeletal remains of *Hemiacodon*, Simpson came to doubt the clear-cut differentiation of tarsioid-lemuroid traits in Eocene primates, saying little, however, about the phylogeny per se of these groups. Through his study of *Hemiacodon* Simpson essentially cast the most serious doubt on the validity of a tarsiiform-lemuriform dichotomy, a view which he espoused again, with even greater persuasiveness, in his 1955 work on the Phenacolemuridae. Simpson's concept in 1940 and 1945 of the Anaptomorphidae included the Omomyinae, Paromomyinae, Anaptomorphinae, Necrolemurinae, and Pseudolorisinae. It is significant that, aside from including several disputed genera and

allocating the Paromomyinae to the family, the Omomyidae of the present work is essentially the Anaptomorphidae of Simpson, 1940 and 1945.

Simpson's studies were not the only ones that cast doubt on the phyletic affinities of the omomyids. In 1946 and 1948 Hürzeler published works on the cranial morphology of *Necrolemur* emphasizing the taxonomic characters of the ear region. His assessment compelled him to suggest that the characters of the anatomy allied *Necrolemur* and relatives with the lemuriforms, rather than with living *Tarsius*. Undoubtedly, Simpson (1955) was influenced by Hürzeler's work, which rekindled doubts voiced in his own 1940 studies. In 1955 he considered the "Anaptomorphidae" not a natural family, and noted that (p. 438), "there is no convincing evidence that any early primate is more 'tarsioid' than 'lemuroid' in natural affinities. The mooted 'tarsioid' characters are some features of the cheek dentition, characters for the most part merely primitive for prosimians and now known (as in the genera just named) to be of possible association with 'lemuroid' skulls; enlargement of the orbits (e.g., in *Tetonius*), which does not reach the *Tarsius* extreme or resemble it in detailed anatomy and which has certainly occurred independently in many primates, especially those that became nocturnal; and in a few cases elongation of the tarsus, which again is not demonstrably like *Tarsius* in extent or detail, which also occurs among 'lemuroids' (or, notably, Lorisiformes, and also among nominal insectivores), and which in some instances at least (e.g., *Hemiacodon*) is different from the truly tarsioid trend and quite surely independent." Thus, in this rather radical departure from the early, turn of the century views on the Eocene primates Simpson, with the full weight of his authority, again cast serious doubt on the previously established probabilities on "prosimian" relationships.

Hürzeler's assertion that the ectotympanic is free in the bulla in *Necrolemur*, contrary to Stehlin (1916) who demonstrated it to be fused to the rim of the bulla, was reinterpreted by Simons and Russell (1960) and Simons (1961b) who suggested that Stehlin's studies on basicranial morphology were correct.

Gazin's (1958) major study on Eocene primates, proposed that the Omomyidae should be separated from the Anaptomorphidae on the family level, making the statement that the genera included in his concept of the Omomyidae (essentially the Omomyinae of this monograph), "are somewhat more primitive or generalized than the anaptomorphids, and in this way occupy a position away from the anaptomorphids towards the notharctids" (p. 47). Later he remarked that even after "the removal of omomyids, the anaptomorphids still appear to be a somewhat unnatural association of genera" (p. 73). In this study Gazin almost completely avoided suprafamilial allocations of the Omomyidae and Anaptomorphidae, although he clearly allocated the Eocene notharctines and adapines to the Lemuroidea. His reluctance may have been partly influenced by the weight of the positive stance of Simpson in 1955, in essence stating that the deciphering of phyletic affinities of Eocene forms is a nearly hopeless undertaking. McKenna (1960), however, in his treatment of the Four Mile tarsiiforms did not follow Gazin and considered the Anaptomorphinae and Omomyinae, as well as the Paromomyinae, as of the same family, i.e., presumably a monophyletic taxon.

In 1961b Simons included the Microchoerinae in the Tarsiidae. His main reason for this allocation was the alleged homologies of the anterior dentition of *Microchoerus* and *Tarsius*. Simons argued in great detail (pp. 57-61) that the only difference in the dental homologies of *Nannopithex*, *Necrolemur*, *Pseudoloris*, and *Microchoerus* from *Tarsius* was that the microchoerines lost the single pair of lower incisors of *Tarsius* and that they possessed a vestigial P_1. Simons has argued that specimens of *Microchoerus edwardsi* showed a small alveolus anterior to the enlarged lower tooth, and concluded that this was proof that the tooth was the canine. With this arrangement he could postulate that *Tarsius* could be derived from a primitive microchoerine with a single pair of lower incisors, canine, and four premolars. Simons also stated that (p. 67), "Some or all of the forms now ranked in the Omomyidae and Anaptomorphidae, may eventually prove to be [tarsioid] (with the advent of new and better specimens) but demonstrating tarsioid charac-

ters . . . becomes increasingly difficult with greater antiquity." In another paper on *Ourayia*, however, Simons (1961a) simply allocated the Omomyidae to the "?Infraorder Lemuriformes" without any further explanation. Simpson's much heeded 1955 statements concerning the Eocene primates undoubtedly influenced students of these forms for several years to come.

Simons (1963, p. 90), in a review discussing the Anaptomorphidae [=Anaptomorphinae], noted that "it is debatable whether anything is gained by ranking this group with the 'tarsioids,' in the absence of sufficient cranial or postcranial remains in this family upon which comparisons could be based." He suggested, however, probable close ties to the Necrolemurinae (= Microchoerinae) which he previously classified within the Tarsiidae. Following Gazin's (1958) remarks on the Omomyidae, *sensu stricto* [=Omomyinae] Simons (1963, p. 94) believed that "Perhaps the closest relationships of this family are to the notharctines, by way of dental resemblances between the early Eocene English species *Cantius eppsi* and North American *Pelycodus* species, but there are also dental features of similarity to the European necrolemurines, and to the Anaptomorphidae."

In the original description of *Rooneyia*, Wilson (1966), tentatively placing the genus into the Omomyidae, classified the family under the infraorder Lemuriformes, being perhaps influenced by the allocation of *Ourayia* to the ?Lemuriformes by Simons (1961a). One year later in 1967 in an important monograph on European early Eocene primates Russell, Louis, and Savage espoused essentially Simpson's 1940 and 1945 concept of the Anaptomorphidae. They included in it the Paromomyinae, Anaptomorphinae, and Omomyinae, but removed the microchoerines into the Tarsiidae, following Simons (1961a).

In a prosimian classification, McKenna, in 1967, considered the Omomyidae and Anaptomorphidae under the superfamily Omomyoidea (in which he also included the Paromomyidae) as separate families. However, following Simons (1961b) he also treated the Microchoerinae as a subfamily of the Tarsiidae, the latter retained in the superfamily Tarsioidea. His various superfamilies were included in the suborder Prosimii and his concept of the Omomyoidea left this group uncommitted to either the tarsiiforms or the lemuriforms. He clearly stated, however, in the notes after the classification that the omomyids were more closely related to the tarsioids than to the lemuroids.

In the following year in 1968, Robinson took the unusual step of placing the Omomyidae within the Lorisiformes. He noted in support of this allocation that it is (p. 308) "most practical . . . because the known characters of the dentition fit that group better than the Tarsiiformes to which they are usually allocated, or than the Lemuriformes where Wilson (1966) has placed *Rooneyia* and by inference the Omomyidae. The Omomyidae seem to me to be farther separated from the Anaptomorphidae than Simpson (1945) or Gazin (1958) would have them. The main reason for grouping the two together is that they are very small, generally Nearctic Primates, with a reduction in the number of premolars . . . If *Rooneyia* is indeed an omomyid then the morphology of the skull is certainly not tarsiiform. Whether it is lorisiform or lemuriform is open to question."

TAXONOMY

The taxonomy of fossil primates or any other diversified groups of small mammals is plagued by a lack of published knowledge, unawareness, or lack of understanding of what is possible and what actually can result morphologically in a deme. This lack of awareness of variation affects both specific and generic categories. The results of faulty taxonomic evaluation go far beyond the boundaries of minor mistakes of taxonomy. Major, synthetic judgments concerning morphological diversity, adaptive radiation, relative taxonomic abundance, number of closely related species living sympatrically at one time, and other important topics on which vertebrate paleontology offers unique contributions to evolutionary biology are all affected by taxonomic decisions.

I have studied the fine collection of Recent

primates, particularly the lemuriforms and lorisiforms, at the American Museum of Natural History to better understand morphological variation in extant demes. As an outgrowth of continual and extended browsing in the collections I noted many striking and interesting cases of both contiguous and disruptive morphological differences, only a few of which can be discussed here. As is often stated, all geological processes must be understood in terms of recent geological events, so the morphological limits of the biological species concept must be based on living species by paleomammalogists who work on small, morphologically relatively homogeneous groups.

Of two specimens of *Galago crassicaudatus* [AMNH (DM) 1161121 and 161122], both represented by skulls and jaws, collected in Tanzania, Mtawamba, at the north end of Lake Manyara, AMNH (DM) 161121 is a male, whereas 161122 is a female. The noted differences, however, are not the result of either sex linkage or sex influence. The M^3 of AMNH (DM) 161122 is roughly triangular in shape and the metacone it bears is quite distinct. A single glance at AMNH (DM) 161121 reveals that M^3 is strikingly different from that of 161122. This tooth, as it completely lacks a metacone, is relatively very transverse and much more reduced in appearance than M^3 seen in AMNH (DM) 161122. It is emphasized again that the two specimens belonged to the same deme. AMNH (DM) 116258 is a female of *Galago crassicaudatus* from Zambia, Balovale. The Tanzanian Lake Manyara and the Zambian Balovale individuals are subspecifically separated. Although many individual differences are apparent, such as the relatively more elongated P^4 and a more distolingually reaching hypocone on P^4 of the Balovale individual, greater dental differences may be noted (and have been above) between two specimens of the Manyara sample than between the two widely separated geographical samples.

The characters noted above may or may not be a continuous feature in *Galago crassicaudatus*. It is very likely, however, that the morphological differences noted for M^3s represent discontinuous variation, a possible manifestation of epigenetic polymorphism (see works by Grüneberg, 1965; Berry, 1963, 1964; Berry and Searle, 1963; etc.). This discontinuous variation, epigenetic polymorphism, is developmental rather than genetic in its origin. Although both the genetics of the organism and the environment play a role, it usually occurs with a certain frequency in a population. Berry and Searle (1963) reported a large number of cases on both cranial and postcranial skeletal material of wild populations of *Sciurus carolinensis*, *Peromyscus maniculatus*, *Lemmus lemmus*, *Microtis agrestis*, *Micromys minutus*, etc.

The type of variability described by Berry (1963, 1964), Berry and Searle (1963), Grüneberg (1965), and others clearly has bearing on taxonomy. It has relevance in making taxonomic decisions often encountered either in large quarry samples or with isolated few specimens from different (or the same) localities. In the case of large samples this should be considered before deciding on the significance of specific kinds of recurring morphological discontinuities in a certain number of specimens from the entire sample. In many instances a "rare species" in a locality may be an epigenetic polymorph of a similar sized, morphologically "homogeneous" large sample of a recognized species. Unfortunately in taxonomic practice it is very difficult to draw the line between continuous or polymorphic variation. The samples are very rarely large enough to allow decision.

Two specimens of *Lepilemur leucopus*, AMNH (DM) 170552 and 170575, both females, from Amboasary, Madagascar, show some interesting extremes of variation worth mentioning. In AMNH (DM) 170552 the distolingual corner of upper molars is subtly, but nonetheless distinctly, more drawn out distolingually than in 170575.

Relative proportions of molar teeth to each other, even when other features were not differentiated, have occasionally played a role in the taxonomic delineation of fossil taxa. Two specimens of *Microcebus* from the same deme, however, are highly instructive concerning these specific and even generic characters. Both AMNH (DM) 174430, female, and 174499, male, were collected in the region of Amboasary, Madagascar. The upper dentitions display the two extremes seen in a blending continuum of size relationship between M^1 and M^2. In 174499 M^1 is

TABLE 1

Distribution of Known Omomyid Localities in North America and Europe

Higher number localities are younger in age. Near synchrony of localities, arranged alphabetically under each number, are indicated by the subscripts attached to the same number. Localities of the 1) category are approximately early Wasatchian and equivalent; the 2) category are medial Wasatchian and equivalent; the 3) category are late Wasatchian and equivalent; the 4) category are early Bridgerian and equivalent; the 5) category are late Bridgerian and equivalent; the 6) category are Uintan and equivalent; and the 7) category are Duchesnean-Chadronian and equivalent ages, respectively.

1) 1a) Avenay (E); 1b) Bitter Creek (NA); 1c) Dormaal (E); 1d) Four Mile (East and West Alheit, Kent, Despair, Timberlake and Sand) Quarries (NA); 1e) Golden Valley (NA); 1f) Gray Bull localities (NA); 1g) Mutigny (E); 1h) Pourcy (E); 1i) Powder River localities (NA); 1j) Red Desert (NA); 1k) Sand Coulee (NA).

2) 2a) Condé-en-Brie (E); 2b) Fossil Butte (NA); 2c) Knight Station (NA); 2d) Lysite localities (NA).

3) 3a) Cuis (E); 3b) Charot (E); 3c) Dad (NA); 3d) Grauves (E); 3e) Huerfano (locs. VI, VIII, IX) (NA); 3f) La Barge (NA); 3g) Lost Cabin localities (NA); 3h) Mancy (E); 3i) Monthelon (E); 3j) San José (NA).

4) 4a) Hiawatha Member (NA); 4b) Egerkingen Huppersand and γ locs. (E); 4c) Geiseltal (Unterkohle) (E); 4d) Huerfano (locs. I, II, III, V, VII, VIIIa) (NA); 4e) Lower Bridger localities (NA); 4f) Messel (E); 4g) Powder Wash (NA).

5) 5a) Bouxwiller (E); 5b) Egerkingen α and β locs. (E); 5c) Geiseltal (Mittelkohle) (E); 5d) Upper Bridger localities (NA).

6) 6a) Badwater locs. (NA); 6b) Poway locs. (NA); 6c) Tapo Ranch (NA); 6d) Uinta locs. (NA).

7) 7a) Chambers Tuff localities (NA); 7b) Duchesne River locs. (NA): 7c) Euzet (E); 7d) Fons (E); 7e) Lower Headon (E); 7f) Pearson Ranch (NA); 7g) Robiac (E).

Abbreviations: E, Europe; NA, North America.

distinctly smaller than M^2, whereas in 174430 M^1 is larger than M^2. Several skulls collected in the same locality show the intermediate form between the two extremes. It is, of course, not my intention to imply that molar size differences should not be used as diagnostic characters, but merely to point out that contrasting extremes may be found in the same deme.

It may be noted here that aside from the section on the History of Investigations, in which names and concepts are presented as used by past authors, I adhere to a strict interpretation of the International Code (Stoll et al., 1961, art. 6) concerning the priority procedures on names of family rank taxa.

ORDER PRIMATES LINNAEUS, 1758

SUBORDER HAPLORHINI POCOCK, 1918

INFRAORDER TARSIIFORMES GREGORY, 1915

FAMILY OMOMYIDAE TROUESSART, 1879

=Omomynae Trouessart, 1879, p. 225.
Omomyinae Wortman, 1904, p. 29.
Omomyidae Gazin, 1958, p. 47.
incl. Anaptomorphidae Cope, 1883, p. 80.
Michrochoeridae Lydekker, 1887, p. 303.
(=Necrolemurinae Simpson, 1940, p. 198. Pseudolorisinae Simpson, 1940, p. 198.)
Tetoniidae Abel, 1931, p. 199.
Teilhardinidae Quinet, 1964, p. 284.

Type Genus. Omomys Leidy, 1869.

Included Taxa. Those included in the subfamilies Anaptomorphinae, Omomyinae, Ekgmowechashalinae, and Microchoerinae.

Geographical and Temporal Distribution. Early Spamacian (early Eocene) to Sannoisian (early Oligocene) of Europe, and early Wasatchian (early Eocene) to late Whitneyan (late Oligocene) of North America.

Family Diagnosis. The family appears to differ from known Tarsiidae, the only other known family of the Tarsiiformes, in having generally slightly reduced canines (but see several genera as exceptions) and incisors enlarged or reduced to varying degrees. Although dentally some genera show either more primitive or more derived characters than the known tarsiids, omomyids known by basicrania differ from the former in having a less enlarged promontory artery and lacking the enlarged hypotympanic sinus of *Tarsius*. The postcranial remains shown by the known bones of *Hemiacodon* are distinctly more primitive than those of *Tarsius*.

The Omomyidae appear to differ from the Paromomyiformes primarily in the relatively greater enlargement of the brain and of the promontory artery and in the modification of the astragalocalcaneal complex. Unlike the primitive paromomyiforms, omomyids do not have the astragalar canal and have posteriorly expanded the tibial trochlea, elongated the lever arm of the calcaneum, and possess a cuboid pivot. Other parts of the skeleton also show considerable advances beyond the paromomyiform level of organization.

There are some consistent differences between the antemolar dentitions of omomyids and paromomyids. The primitive condition in omomyids is the presence of a distinct protocone on P^3 as on P^4, i.e., a transversely wide tooth. This condition is matched in both the plesiadapid-carpolestid groups and in adapids, perhaps suggesting the omomyid condition to be primitive and the paromomyid one, in which P^3 is without a well-defined protocone, the derived primate feature.

The external ectotympanic, varying degrees of petromastoid inflation, the point of entry of the internal carotid on the medial side of the bulla, and the specializations of the tarsus together distinguish the omomyids from known adapids, the most primitive group of the known strepsirhines. For further details see Phylogeny and Classification.

SUBFAMILY ANAPTOMORPHINAE COPE, 1883

Anaptomorphidae Cope, 1883, p. 80.
Tetoniidae Abel, 1931, p. 199.
Anaptomorphinae Simpson, 1940, p. 198.
Teilhardinidae Quinet, 1964, p. 284.

Type Genus. Anaptomorphus Cope, 1872.

Included Taxa. Tribe Anaptomorphini Cope, 1883, and tribe Trogolemurini, new.

Geographical and Temporal Distribution. Sparnacian of Europe and Wasatchian of North America (early Eocene) and early Bridgerian (early medial Eocene) of North America.

Subfamily Diagnosis. The Anaptomorphinae are much less diverse or numerous than the Omomyinae. They represent the earliest known species of the family and the dental morphotype for the subfamily suggests them to be dentally perhaps somewhat more primitive than the Omomyinae. Taxa in this subfamily appear to be characterized by the presence of a protocone-fold (sometimes referred to in the literature as *Nannopithex*-fold), and a type of hypocone that is an indistinct elevation on the distal slope of the protocone. This latter character appears in the Microchoerinae and occasionally, probably as a primitive character, in the Omomyinae. Along with this type of hypocone construction anaptomorphines are usually also characterized by low and relatively bulbous trigonid cusps and relatively shallow talonids. See also diagnosis of the Omomyinae below.

Discussion. It seems clear that the *Tetonius-Absarokius* group, *Anemorhysis* spp., and particularly *Trogolemur* had a distinctly enlarged anterior incisor. A clear absence of this condition in either *Teilhardina* or *Anaptomorphus*, then either as a result of reduction of the enlarged state or as a retention of the primitive one, would argue against singling out the Anaptomorphinae as a natural group adaptively distinct on the family level. Incisor enlargement cannot be used as a diagnostic feature of this probably monophyletic subfamily.

TRIBE ANAPTOMORPHINI COPE, 1883

Anaptomorphidae Cope, 1883, p. 80.

Type Genus. Anaptomorphus Cope, 1872.

Included Taxa. Subtribe Teilhardinina Quinet, 1964, subtribe Anaptomorphina Cope, 1883, and subtribe Tetoniina Abel, 1931.

Tribal Diagnosis. Anaptomorphines not having a combination of the following characters: extremely enlarged anterior incisor extending under the molars, extremely reduced canines, and lack of an M_3 relatively longer than the more anterior molars. Lack of these specializations separates the Anaptomorphini from the Trogolemurini.

SUBTRIBE TEILHARDININA QUINET, 1964

Teilhardinidae Quinet, 1964, p. 284.

Type Genus. Teilhardina Simpson, 1940.

Included Taxa. Type genus and *Chlororhysis* Gazin, 1958.

Subtribe Diagnosis. Primitive anaptomorphinines with low, premolariform fourth premolars, unreduced second lower premolars, and

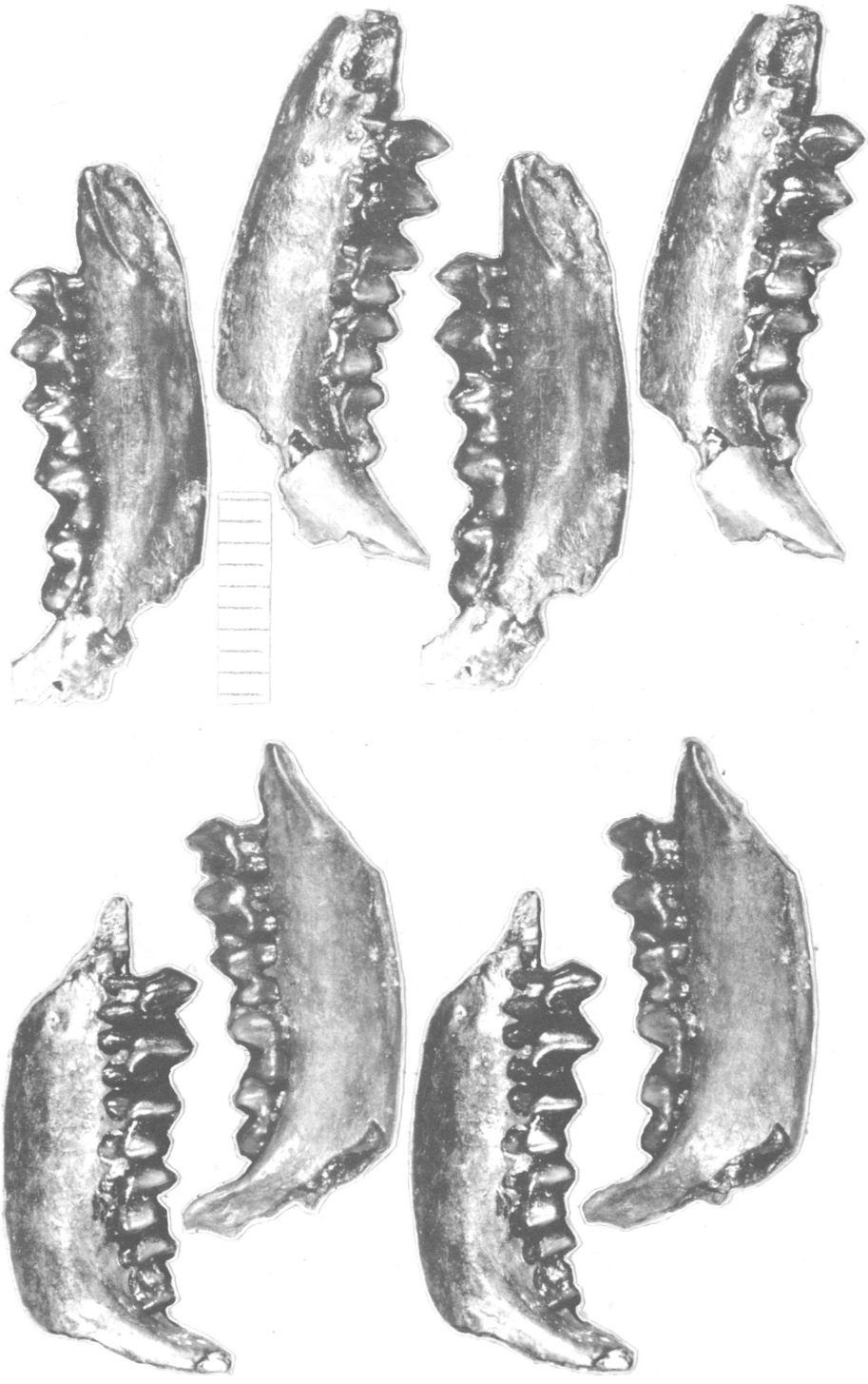


FIG. 1. *Teilhardina belgica*, IRSNB 64, type, left P_3-M_3 (above) and IRSNB unnumbered, left horizontal ramus with P_3-M_3 (below), both from Dormaal. Stereophotographs: above left and below right medial, and above right and below left lateral views, respectively. Subdivisions on scale represent 0.5 mm.

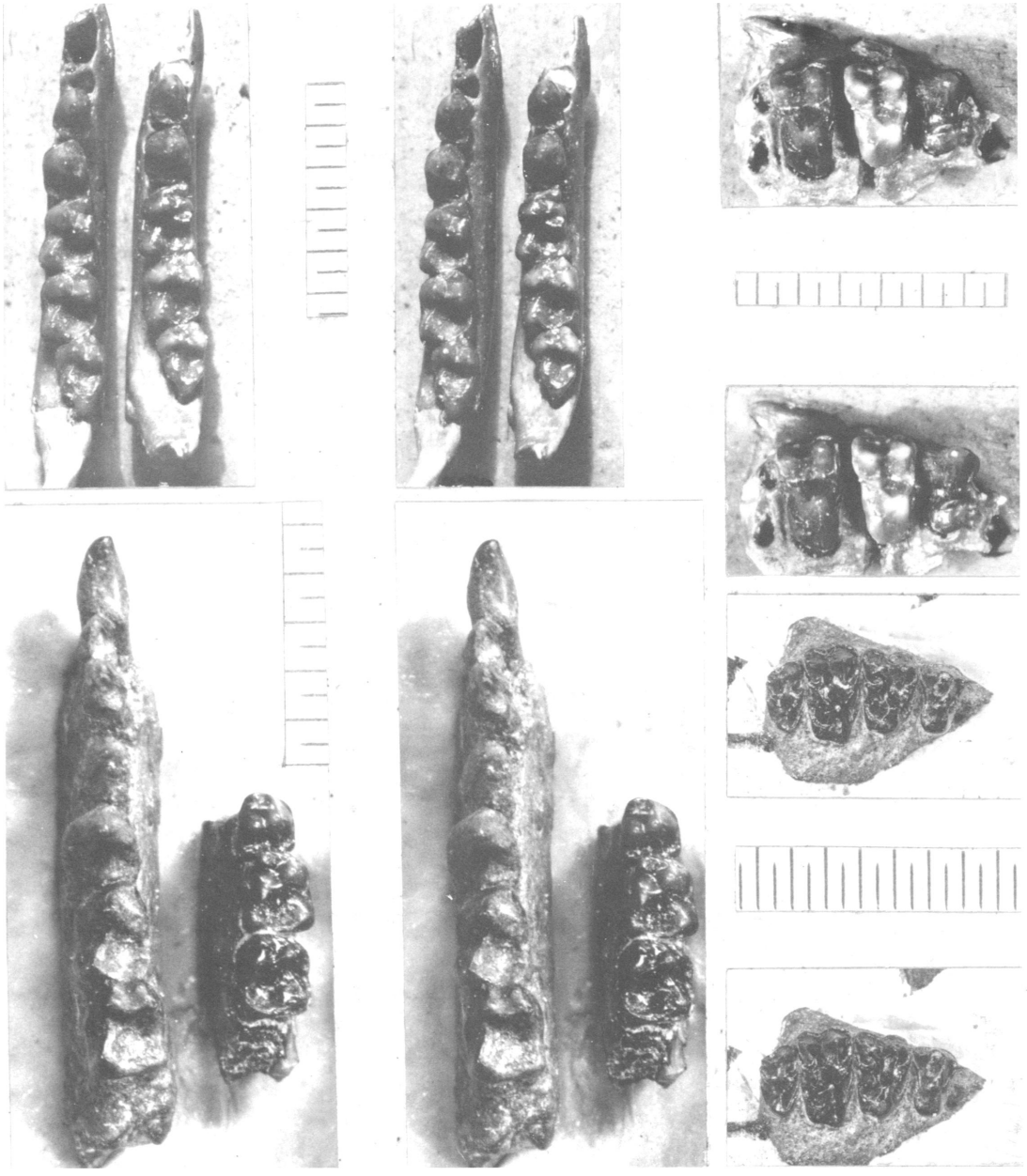


FIG. 2. *Teilhardina belgica*, IRSNB 64, type, Dormaal, left horizontal ramus with alveoli for I_1 and I_2, C, P_1 and P_2, and the teeth P_3-M_3 (above left); IRSNB unnumbered, left horizontal ramus with alveoli for C, P_1 and P_2, and teeth P_3-M_3 (above center); IRSNB 1272, right P^4-M^2 (above right). *Tetonius* sp., UCMP 46192, East Alheit Pocket, Wasatch beds, left I_1-C, space for P_2, and P_3-M_3 (below left). *Anemorhysis tenuiculus*, AMNH 15066, Gray Bull beds, right P_4-M_2 (below center); PU 13027, type, Gray Bull beds, right P^4-M^3 (below right). Stereophotographs: occlusal views. Subdivisions on scales represent 0.5 mm.

not very reduced canines and unenlarged incisors. These genera are perhaps the most primitive representatives of the Anaptomorphinae, possibly of the entire Omomyidae.

Discussion. It is possible that once the phylogeny of the Omomyidae is better understood teilhardinines may be found to be more recently related to omomyines than to the remaining Anaptomorphinae.

TEILHARDINA SIMPSON, 1940

Omomys Teilhard de Chardin, 1927, p. 16.
Protomomys Teilhard de Chardin, 1927, p. 25 (petitioned to be suppressed, see McKenna, Russell, and Savage, 1969).
Teilhardina Simpson, 1940, p. 190.

Type Species. Teilhardina belgica (Teilhard de Chardin, 1927).

Included Species. Type species only.

Geographical and Temporal Distribution. Sparnacian (early Eocene) of Belgium.

Generic Diagnosis. Anaptomorphines differing from other members of the subfamily in having the largest number of teeth known in the group, although P_1 appears to be all but lost from the small, laterally crowded alveolus. Unlike the small canine of *Tetonius*, *Anaptomorphus*, *Anemorhysis*, or *Chlororhysis*, *Teilhardina* retained an apparently primitively large canine.

Discussion. Based on the total available morphology of this genus there seems little doubt that it is a close relative of the Eocene tarsiiforms as stated or implied by Teilhard de Chardin (1927) and Simpson (1940).

Whether *Teilhardina* should be placed within the Anaptomorphinae or the Omomyinae is difficult to decide. It has been been traditionally placed with omomyines (former Omomyidae *sensu stricto*), and Russell, Louis, and Savage (1967, p. 8) stated that: "no one has offered serious arguments against it being an omomyine, a group often cited for its primitiveness and for possible ancestral position with respect to anaptomorphids, microchoerines, and ceboid monkeys." These authors have also stated (p. 17) that, "the resemblances of *Teilhardina* to *Pseudoloris* suggest that the latter had ancestry in the omomyines." Simons (1972, pp. 1953-1954) has restated previous views that *Teilhardina* is phyletically closer to the omomyines than to the group traditionally considered Anaptomorphinae.

A detailed comparison of specimens of *Teilhardina belgica* with both early Eocene anaptomorphines and *Omomys* and *Loveina* indicates a more recent affinity of the European genus with forms like *Chlororhysis*, *Anemorhysis*, and *Tetonius*. This conclusion is based on various features derived from dental comparisons. Unlike *Omomys*, but like *Anemorhysis* and *Tetonius*, the upper molars of *Teilhardina* bear a distinct protocone-fold, admittedly a primitive character. M^3 of *Teilhardina*, like those of the anaptomorphines compared, are reduced and mesiodistally constricted, a derived character state. M^3 of both *Loveina* (admittedly a referred specimen, MCZ 3495) and *Omomys* are large and not constricted mesiodistally. I judge the base of the trigonid cusps of *Teilhardina* to be considerably inflated as in anaptomorphines, although not to the degree seen in either *Anemorhysis* or *Tetonius*. In *Omomys* or *Chumashius* there is virtually no basal inflation of the trigonid cusps. Perhaps not significantly, as in *Tetonius*, but unlike in *Omomys*, the hypoconulid in *Teilhardina* is closer to the hypoconid than to the entoconid.

P_4 of *Teilhardina* is semimolariform, i.e., with a distinct metaconid and paraconid, as apparently is the primitive condition in both omomyid subfamilies. Like *Anemorhysis*, for example, it lacks the elongated paracristid of *Omomys*.

The dental morphology strongly suggests a more anaptomorphine than omomyine character complex for *Teilhardina*. It is also apparent that the unreduced canines and incisors, which were not enlarged, were probably the primitive condition for the Eocene subfamilies of the Omomyidae and for the family also.

Simpson (1940, p. 190), who was the first to advocate the generic distinctness of *Teilhardina*, has justifiably emphasized the importance of this genus. He failed, however, to consider the calcaneum allocated by Teilhard de Chardin (1927, fig. 14) to this genus and as a result he has overemphasized the overall ancestral nature of this taxon for the primates.

Adaptations. Adaptational assessment of *Teilhardina* is very difficult largely because it is in

many ways an extremely primitive omomyid. In spite of the fact that the teeth are in most ways primitive, the third molars show signs of reduction from a relatively larger ancestral condition. The lower canine was large, and a vestigial P_1 was present. The lingual slope of the protocone is very extensive, probably an ancestral primate character but perhaps a secondary acquisition of this feature by *Teilhardina*.

The jaw presents an interesting morphology not seen in other omomyids. The loose symphysis was nearly horizontal, forming a very low angle with the inferior border of the horizontal ramus, and in general the mandible anterior to P_3 is very shallow. This is in particular contrast to the relatively great depth of the mandible under M_2 and M_3. Based on all this evidence I judge *Teilhardina belgica* to be insectivorous.

Teilhardina belgica (Teilhard de Chardin, 1927)
Figures 1-4; Table 2

Omomys belgicus Teilhard, 1927, p. 16.
Teilhardina belgica (Teilhard, 1927), Simpson, 1940, p. 190.

Type. (*Lectotype*). IRSNB 64, left mandible fragment with P_3-M_3; from Dormaal beds (Sparnacian lower Eocene), Belgium.

Hypodigm. The type and IRSNB 56-59, 61, 1164, 1165, 1262, 1263, 1269, 1272, 4317, 4325, 4385-4389, and a large number of isolated upper and lower teeth from the type locality.

Geographical and Temporal Distribution. Same as for the genus.

Specific Diagnosis. Only known species of the genus.

Dental Formula. $I\frac{1,2}{1,2}$; $C\frac{1}{1}$; $P\frac{1,2,3,4}{1,2,3,4}$; $M\frac{1,2,3}{1,2,3}$.

Discussion. Since the original description of this species by Teilhard de Chardin (1927) many new specimens have been collected at the same locality (Quinet, 1966). The two best mandible fragments have been figured by Teilhard de Chardin (1927, figs. 12, 13), and Quinet (1966, p. 1) has published photographs of the best maxilla fragment (IRSNB 1272). I restudied these specimens along with the remaining hypodigm in 1968. Figures 1-4 show these specimens in addition to a synthesis of the entire mandibular and dental evidence known for this species.

There were several specimens placed into the original hypodigm by Teilhard de Chardin, which obviously did not belong to this species. In addition to referring a rodent-like astragalus and a frog humerus (Teilhard de Chardin, 1927, fig. 14b, c) he allocated a left lower jaw (his fig. 13, bottom) with P_4 to *Teilhardina belgica*. In 1964 Quinet referred the latter mandible to *Dormaalius vandebroeki*, an alleged tupaioid, called new both in 1964 and 1969 and placed by this author into the new family Dormaaliidae.

Various new postcranial elements of this species, discovered in miscellanea of the Dormaal collection in 1972, will be discussed in another work, although some features of the astragalocalcaneal complex are illustrated (figs. 156-159) and discussed under Phylogeny and Classification and Adaptations.

This species is undoubtedly one of the most important among early Tertiary primates because: a) it is one of the most primitive of known primates in retaining P_1 and a relatively primitive primate molar morphology; b) its occurrence in Europe during the earliest Eocene; and c) it is a dentally relatively primitive taxon with advanced postcranial morphology, as this is judged from the astragalus and calcaneum. Whether it is ancestral to the Anthropoidea (Platyrrhini and Catarrhini), as Quinet (1966) stated it, is a moot point at present, although the nature of calcaneal advancement of the genus would perhaps argue against this.

It may be noted that Simons's (1972, p. 157) recent illustration of *Teilhardina belgica* lacks some details, such as the protocone-fold, the presence of which is a characteristic of the European omomyid.

CHLORORHYSIS GAZIN, 1958

Chlororhysis Gazin, 1958, p. 27.

Type Species. Chlororhysis knightensis Gazin, 1958.

Included Species. Type species only.

Geographical and Temporal Distribution. Late Wasatchian (late early Eocene) of Wyoming.

Generic Diagnosis. Very faint or absent cingulids along with small metaconid on P_4 appear to set this group aside from *Anemorhysis* and *Teilhardina*, the most similar taxa within the

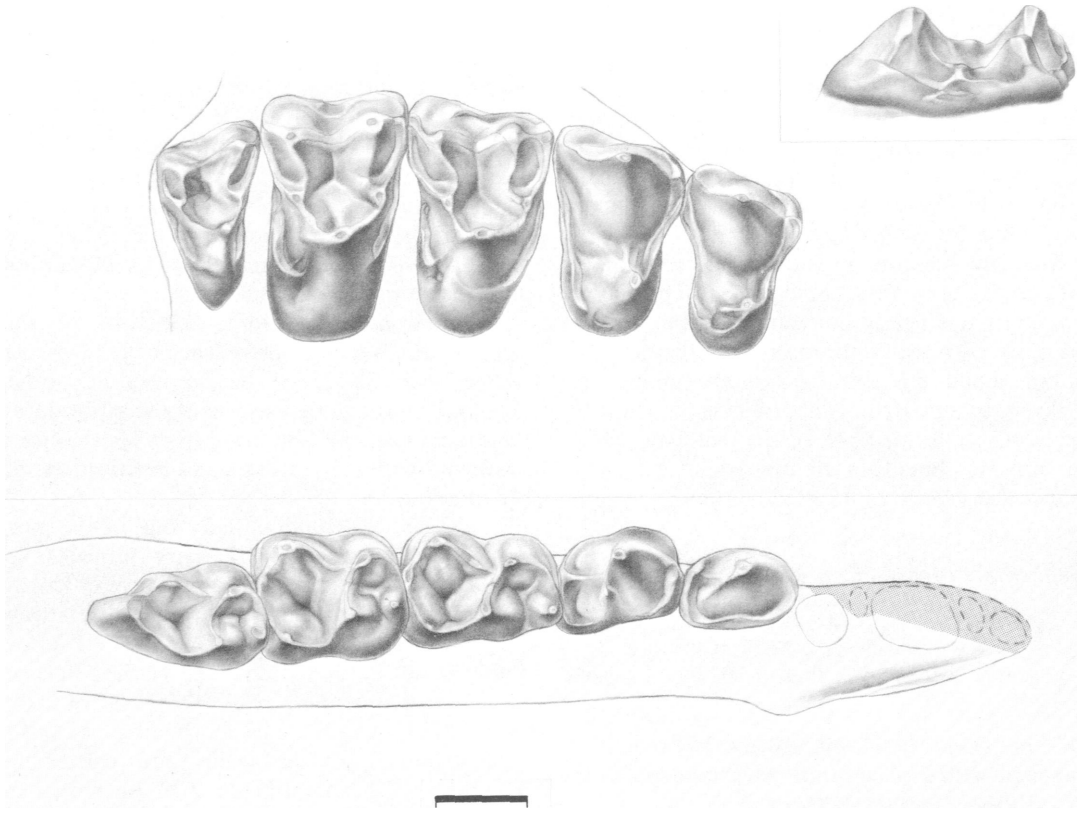


FIG. 3. *Teilhardina belgica*, upper dentition based on IRSNB 56, 58, 59, 1269, and 4325 and horizontal ramus and lower dentition based on IRSNB 64, type, Sparnacian of Belgium, right P^3-M^3 (above) and left horizontal ramus with P_3-M_3 (below); occlusal views. Reconstruction shown by uniform stippling and broken lines. Scale represents 1 mm.

Anaptomorphinae. The two incisors were not so large as those in either *Anemorhysis* or *Tetonius* and the canine is relatively larger than in either of the latter. Molar characters, because of uncertainty of association, are not used in this diagnosis.

Discussion. Gazin (1958, p. 27) considered *Chlororhysis knightensis* to be an omomyid, *sensu stricto* (i.e., an omomyine) and suggested that an eventual synonymy with *Loveina* might be warranted. He predicted that a discovery of the lower molars will prove them to be omomyine rather than anaptomorphine, "like those of *Loveina*, or possibly those of *Utahia*" (p. 27). In 1962 when Gazin allocated, correctly I believe, UCMP 46750 to *Chlororhysis*, he firmly established the generic distinction of this genus from *Loveina*, but he continued considering it an omomyid, *sensu stricto.*

In 1967 in their discussion of the Omomyidae, Russell, Louis, and Savage suggested contrary to Gazin that *Chlororhysis* was an anaptomorphine rather than an omomyine. Simons (1972, p. 146) included *Chlororhysis*, along with *Anemorhysis*, in *Tetonius* and cited views allegedly held by me which corroborated his stand. The possibility of such a taxonomic action was noted by Simons in a conversation in 1969, a view which at that time I chose not to dispute. This occasion was the provenance of my alleged views.

The type specimen of the only known species

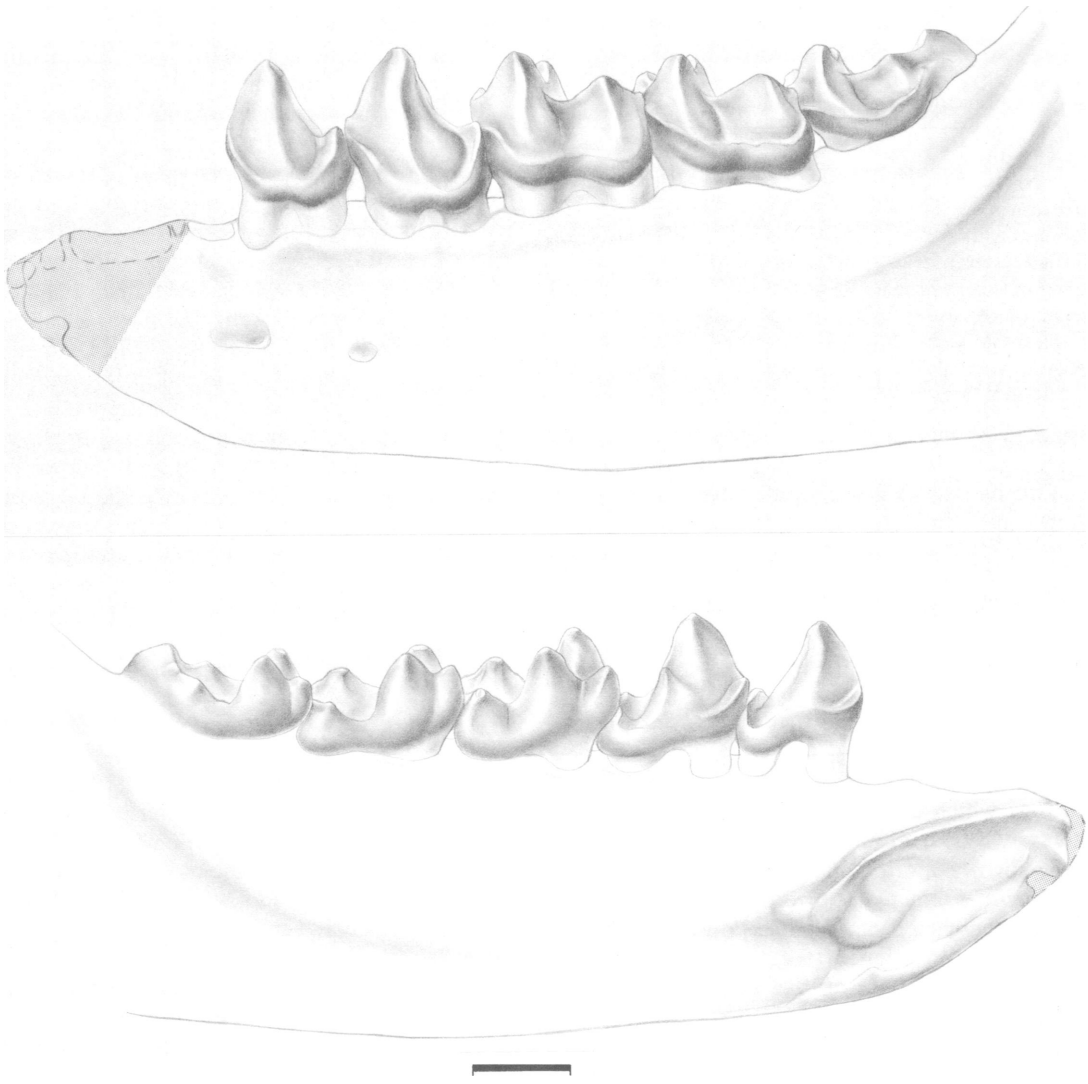


FIG. 4. *Teilhardina belgica*, left horizontal ramus with P_3-M_3, based on IRSNB 64, type, Sparnacian of Belgium; lateral (above) and medial (below) views, respectively. Reconstruction shown by uniform stippling. Scale represents 1 mm.

shows this taxon to be dentally possibly one of the most primitive omomyids in North America. The allocation of UCMP 46705, if the latter is correctly referred, leaves no doubt that *Chlororhysis knightensis* is an anaptomorphine rather than an omomyine. The base of the trigonid cusps is distinctly bulbous and the relatively shallow talonid basins of *Chlororhysis* compared, for example, to the similar aged and similar sized *Loveina*, and the anaptomorphine M_3, as in *Anemorhysis* and *Tetonius*, strongly suggest anaptomorphine rather than omomyine ties.

There are some differences between the P_4 construction of *Chlororhysis* and *Loveina*, the

TABLE 2
Numerical Data on Tarsals of *Teilhardina belgica*

Calcaneum	IRSNB 4385	4387	4389	4390	61	*N*	OR	M
Total length	6.9	–	7.3	6.75	6.5	4	6.5 -6.9	6.79
Lever arm	3.35	3.4	3.45	3.3	3.1	5	3.1 -3.45	3.32
Load arm	3.5	–	3.8	3.3	3.2	4	3.2 -3.8	3.45
Calcaneal width at sustentacular facet	2.5	2.1	2.6	2.25	2.35	5	2.1 -2.6	2.36
Height of tuber calcanei	2.3	2.0	2.2	2.0	2.0	5	2.0 -2.3	2.10
Length of astragalo-calcaneal facet	1.5	1.5	1.6	1.5	1.5	5	1.5 -1.6	1.52
Height of astragalo-calcaneal facet	0.85	0.9	0.9	0.95	0.85	5	0.85-0.95	0.90
Astragalus	IRSNB 4386							
Width of tibial trochlea	1.85	–	–	–	–	–	–	–
Length of body	2.35	–	–	–	–	–	–	–
Width of body	2.45	–	–	–	–	–	–	–
Width of head	1.8	–	–	–	–	–	–	–
Length of sustentaculo-naviculoastragalo facet	2.8	–	–	–	–	–	–	–
Height of body	2.3	–	–	–	–	–	–	–
Height of head	1.2	–	–	–	–	–	–	–
Total length	4.35	–	–	–	–	–	–	–

genus to which *Chlororhysis* was originally compared by Gazin (1958). The most outstanding is the slightly more molarized character of P_{3-4} of *Loveina* compared with that of *Chlororhysis*, but these characters alone might not be sufficient for generic separation of the two genera. If the referred specimen from the Lost Cabin aged sediments in the "Hiawatha Mbr." of the Wasatch Formation is *Chlororhysis knightensis*, then the molar differences noted clearly warrant generic separation of *Chlororhysis* from *Loveina*.

The known lower molars, belonging to a referred specimen, show that the construction of the trigonids in the only known species of this genus is similar to the condition displayed by *Anemorhysis* spp., *Tetonius* spp., and *Absarokius* spp., in having the bulbous-based, somewhat crowded cusps, perhaps the primitive anaptomorphine complex of characters. This is unlike the less inflated trigonid cusp morphology of omomyines, such as *Chumashius*, *Omomys*, or *Uintanius*.

Adaptations. The incisors inferred from the position and size of the alveoli were moderate-sized, not enlarged like those of *Tetonius homunculus*, *Anemorhysis* spp., or *Absarokius* spp. Both the paraconids and the metaconids are low and a lingual cingulid passes between these cusps on P_3 and P_4. Lingual cingulids are prominent on both P_2 and the canine. The latter, a premoliariform rather than a caniniform tooth, is mesially elongated with a fairly long cutting edge (paracristid). The apex of the canine is not appreciably pointed.

There are two features of the canine, providing the homology of the tooth is correct, which are suggestive of the dental adaptations of *Chlororhysis*. The canine is a small tooth and not very pointed or piercing. The well-developed lingual cingulum, as well as the crown morphology, makes this tooth part of the premolar series rather than a tooth with canine functions. Much of what may be said of the adaptations of the antemolar teeth depends on the assessment of

the incisors of the species. Although, judged from the alveoli, two incisors were present and neither was very enlarged, lack of actual teeth prevent any further judgment. Yet the lack of very enlarged incisors and the presence of a short-crowned, premolariform canine are poor mechanical equipment for food procurement which might involve habitual piercing of live prey. This, of course, is not a statement that *Chlororhysis knightensis* was not habitually insectivorous. It is merely an interpretation of the meager evidence that the mechanical requirements usually associated with habitual prey catching and killing do not appear to be present.

The symphysis on the holotype of the genero-type is not so horizontal as, for example, that of *Teilhardina*. In addition to the inferior transverse torus, a bony shelf above the former, a superior transverse torus, suggests that transverse forces were perhaps habitually incurred. The symphysis was clearly mobile.

Chlororhysis knightensis Gazin, 1958
Figures 5-8

Chlororhysis knightensis Gazin, 1958, p. 27.

Type. USNM 21901, left mandible fragment with C-P_4; collected from upper Wasatch (Knight) beds, south side of Milleson Draw, east side of Green River, NW½ sect. 4, T 28 N, R. 111 W. Sublette Co., the provenance of the La Barge assemblage (Gazin, 1958).

Hypodigm. The type and UCMP 46705, the latter collected from sediments of the "Hiawatha Mbr.," main body of the Wasatch, approximately 100 feet below the Tipton tongue (late early Eocene, approximately Lost Cabin equivalent) of the Washakie Basin, south of Sheel Creek Rd. (loc. V5721 of the University of California, Department of Paleontology), near Dad, Wyoming.

Geographical and Temporal Distribution. Same as for genus.

Specific Diagnosis. Only known species of the genus.

Dental Formula. $I\frac{1,2}{1,2}; C\frac{1}{1}; P\frac{2,3,4}{2,3,4}; M\frac{1,2,3}{1,2,3}$.

SUBTRIBE ANAPTOMORPHINA COPE, 1883

Anaptomorphidae Cope, 1883, p. 80.

Type Genus. Anaptomorphus Cope, 1872.

Included Genera. Type genus only.

Subtribe Diagnosis. Anaptomorphines with relatively large molars, relatively small anterior dentition, and short, U-shaped jaws.

Discussion. The most significant diagnostic difference of the Anaptomorphina from the other subtribes of the Anaptomorphini is the derived nature of the anterior jaw configuration and anterior dentition. Unlike the enlarged first incisor in the Tetoniina or the primitively large canine of *Teilhardina*, the Anaptomorphina show a different anterior dentition. This is distinct from the other groups largely in its inferred lack of differentiation between the incisors and canines, at least as far as their relative sizes are concerned. I suspect this condition is derived from a teilhardininan or primitive tetoniinan pattern, specialized in a direction different from either group.

ANAPTOMORPHUS COPE, 1872

Anaptomorphus Cope, 1872, p. 554.
Euryacodon: Wortman, 1904, p. 139.

Type Species. Anaptomorphus aemulus Cope, 1872.

Included Species. Type species and *A. westi*, new species.

Known Distribution. Bridgerian (medial Eocene) of Wyoming.

Generic Diagnosis. Anaptomorphines differing from *Tetonius* and *Absarokius* in having P_4 approximately the same height as the first lower molar. They differ from *Anemorhysis* and *Chlororhysis* in lacking a metaconid on P_4 and from all other anaptomorphines, except *Chlororhysis* and *Teilhardina*, in having relatively small lower incisors.

Discussion. Judged by the size of teeth, the specimens from the Tree Road, Hawk, and Fault localities of West (1973) appear to form a cluster on the large end of the spectrum, whereas the "*A. wortmani*" group (see discussion under *A. aemulus*), an artificial sample from lower Bridger beds, cluster on the small end of this continuum. I do not consider "*A. wortmani*" valid but I do consider the size differences between specimens of *A. aemulus* and the sample from West's localities worthy of species rank differences.

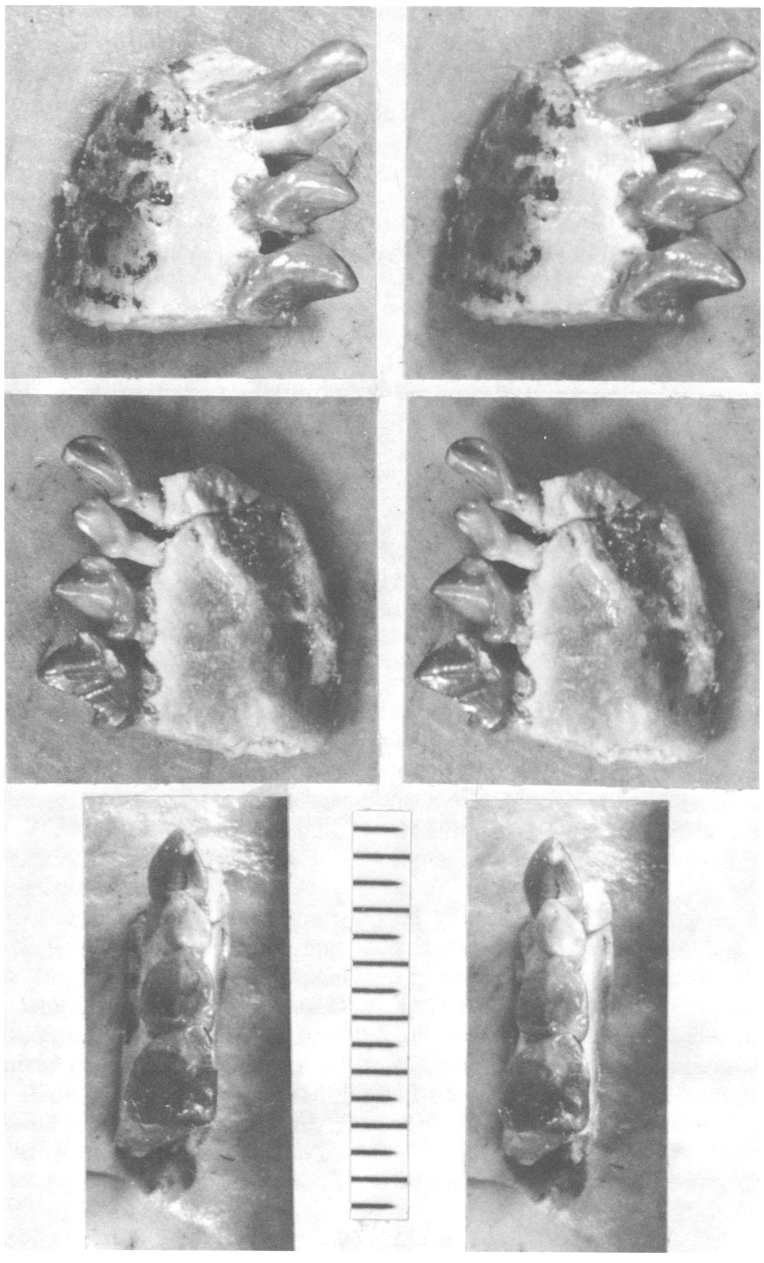


FIG. 5. *Chlororhysis knightensis*, USNM 21901, type, upper Wasatch beds, left C-P_4. Stereophotographs: above lateral, middle medial, and below occlusal views, respectively. Subdivisions on scale represent 0.5 mm.

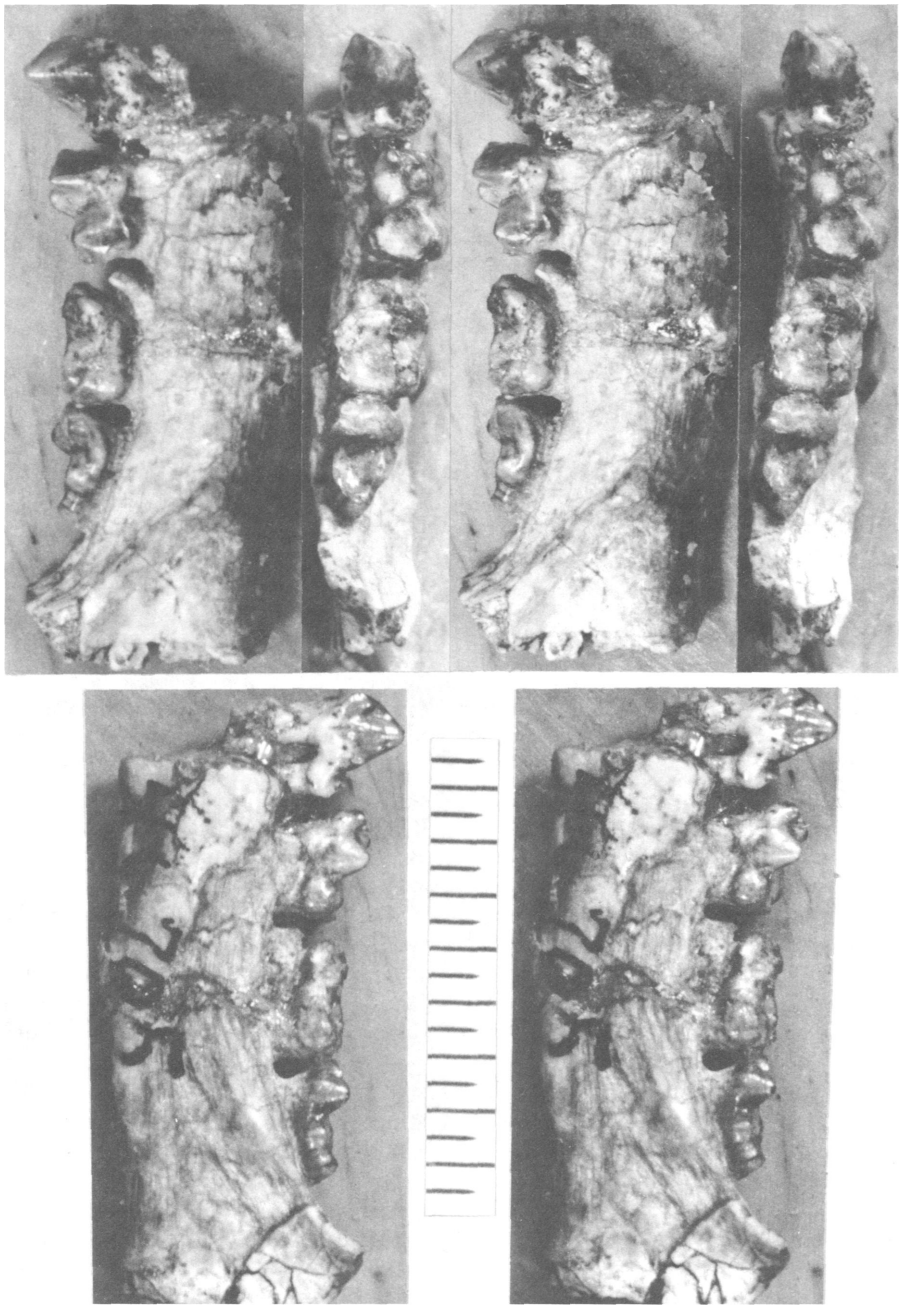


FIG. 6. *Chlororhysis knightensis*, UCMP 46705, upper Wasatch beds, right P_4-M_3. Stereophotographs: above left lateral, above right occlusal, and below medial views, respectively. Subdivisions on scale represent 0.5 mm.

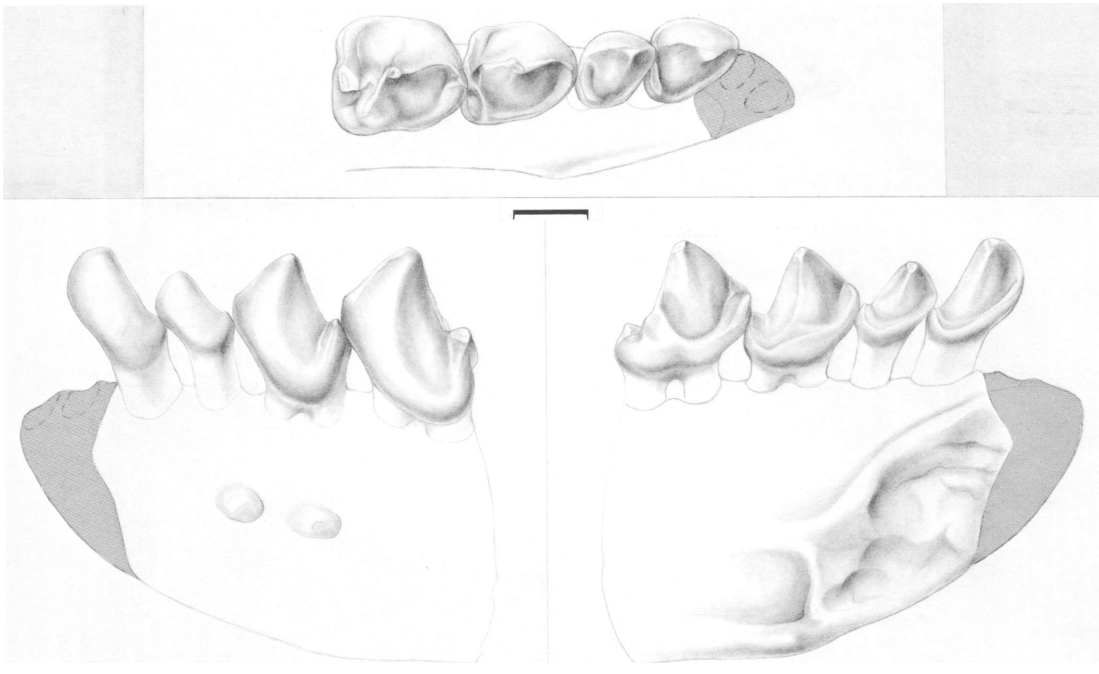


FIG. 7. *Chlororhysis knightensis*, left mandible fragment with C-P_4, based on USNM 21901, type, late Wasatchian of Wyoming; occlusal (above), lateral (below left), and lingual (below right) views, respectively. Reconstruction shown by uniform stippling and broken lines. Scale represents 1 mm.

Both species of *Anaptomorphus* appear to be very similar in their total morphology to *Tetonius homunculus*, and derivation from a species similar to the latter or a form like it with a P_2 and an unenlarged P_4 is likely. A considerable gap exists in the knowledge of the history of *Anaptomorphus*. During the time interval represented by Lysite and Lost Cabin sediments neither the ancestry nor *Anaptomorphus* are known as yet.

From the start it has been obvious from the CV values of the combined samples (see table 3) that the size range represented spans of more than one species. In order to help determine the taxonomic status of the various samples of *Anaptomorphus* a series of t-tests were calculated. The t-tests between the type of *A. aemulus* and the "*A. wortmani*" sample (YPM specimens of table 4) show no significant values. The differences between the combined *A. aemulus* sample [i.e., which includes the YPM specimens allocated to *A. wortmani* by Gazin (1958)] and the *A. westi* sample appear to be significant (t=8.405; P 0.001). The sample of two specimens from the Big Sandy local fauna is enigmatic (see fig. 9); it may represent *A. aemulus*.

FM 15661, a left maxilla with M^{1-3} of *A. westi*, is the first known specimen of *Anaptomorphus* showing the morphology of the upper molars. As expected from the lower molars, the upper ones are similar both to *Tetonius homunculus* and *Absarokius* spp. The last molar, as in the latter, is considerably reduced and M^2 is strikingly larger than M^1. As in the other anaptomorphines cited, the lingual slope of the protocone is long and gently sloping. The relief, in general, is low on the molars and the crest, originating from the protocone and oriented distally, making up essentially the cutting edge of the hypocone, is extensive. In general, the molars are slightly less wide transversely than those of *Tetonius homunculus*, but quite similar in proportions to those of *Absarokius* spp.

Adaptation. Anaptomorphus combines primitive molar and premolar (at least the fourth, which is the only one known) morphology with a

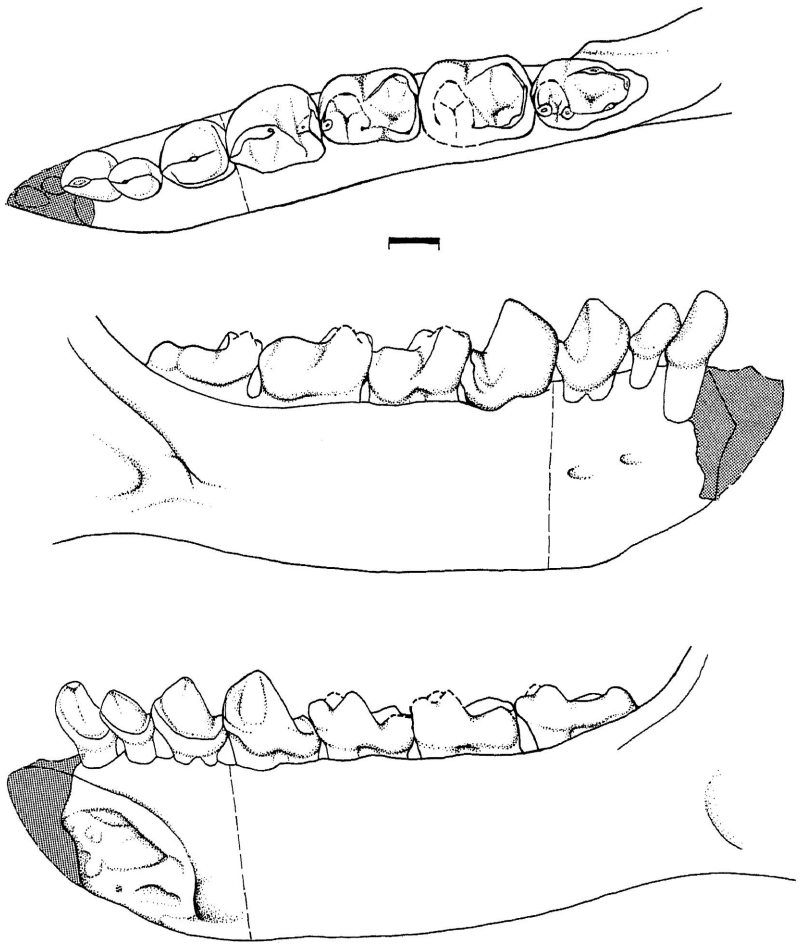


FIG. 8. *Chlororhysis knightensis*, hypothetical reconstruction of right mandible with C-M_3, based on USNM 21901, type, and UCMP 46705, late Wasatchian of Wyoming; occlusal (above), lateral (middle), and medial (below) views, respectively. The broken line anterior to P_4 represents the reconstructed contact between two moieties, reconstructed from the first and second specimens listed, respectively. For details see the discussion under *Chlororhysis*. Reconstruction shown by uniform stippling and broken lines. Scale represents 1 mm.

reduced dentition that appears to have been arranged in a nearly U-shaped manner. Alveoli of the teeth anterior to P_4 show that the roots were buccolingually wide and mesiodistally constricted. The dimensions of the alveoli indicate that stresses to the mandible were transversely directed. The unusually extensive inferior transverse torus also lends support to this inference. Emphasis in this genus is clearly on the cheek teeth, particularly the first and second molars; the molars are low-crowned and the protocone crest is very well developed. The dentition suggests that this small form was a frugivore, and only marginally insectivorous.

Anaptomorphus aemulus Cope, 1872
Figures 9-11; Tables 3, 4

Anaptomorphus aemulus Cope, 1872, p. 554.
Euryacodon lepidus: Wortman, 1904, p. 139.
Anaptomorphus wortmani Gazin, 1958, p. 76.

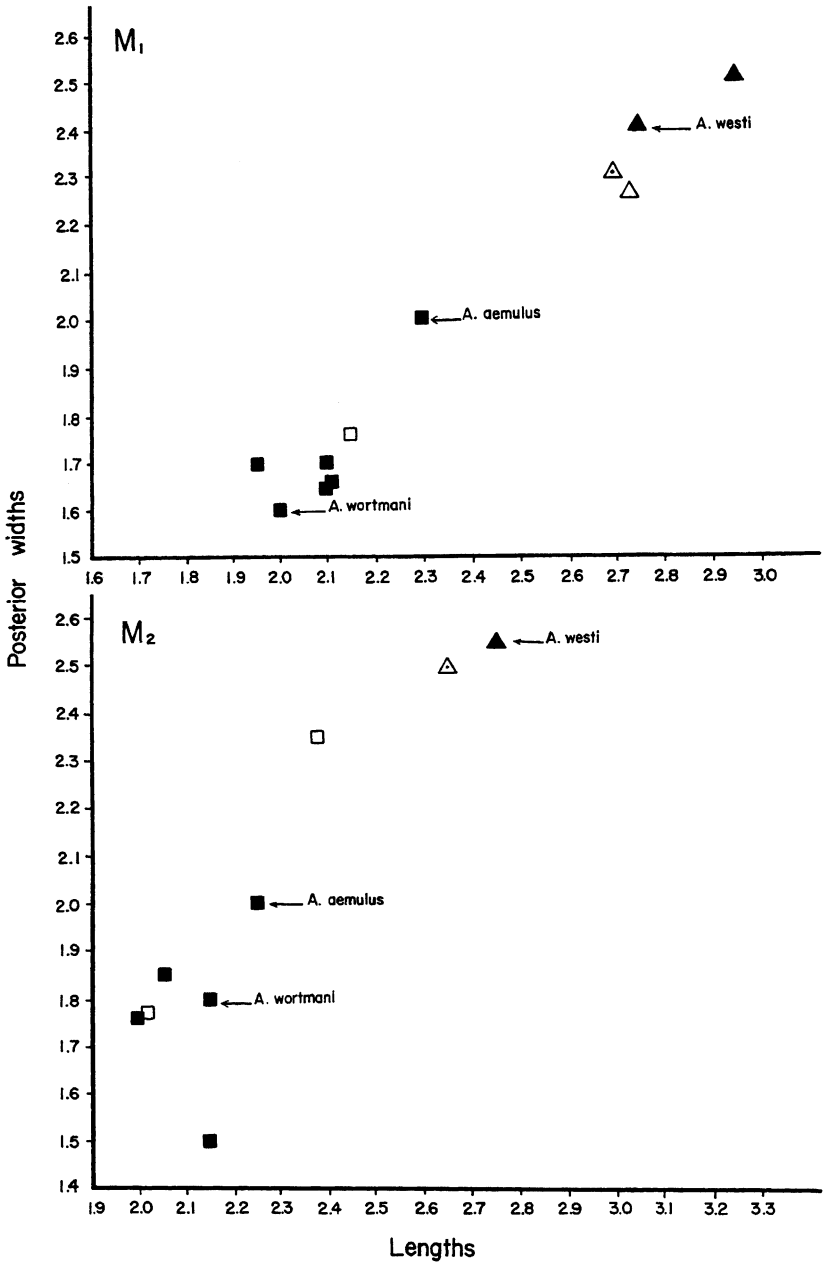


FIG. 9. Scattergrams of the posterior width/length of M_1 (above) and of M_2 (below) of various samples of *Anaptomorphus*. The arrows point to plots of the holotypes of stated species. The symbols represent the following Bridgerian localities: black square, lower Bridger beds; clear square, Big Sandy beds; black triangle, West's Hawk locality, triangle with dot, West's Tree Road locality; clear triangle, West's Fault locality.

TABLE 3
Numerical Data for the Combined Sample of *Anaptomorphus*

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P_4								
L	1	2.20	–	–	–	–	–	–
PW	1	2.00	–	–	–	–	–	–
AW	1	2.20	–	–	–	–	–	–
L/PW	1	1.10	–	–	–	–	–	–
M_1								
L	12	1.95-2.80	–	2.308±0.081	0.280±0.057	12.395±2.530	0.377	−1.291
PW	12	1.60-2.60	0.959	2.005±0.107	0.372±0.076	18.941±3.866	0.385	−1.666
AW	12	1.50-2.20	0.890	1.808±0.078	0.271±0.055	15.311±3.125	0.157	−1.808
L/PW	12	1.00-1.27	–	1.165±0.025	0.087±0.018	7.596±1.550	−0.332	−0.696
M_2								
L	9	2.00-2.70	–	2.269±0.091	0.274±0.065	12.402±2.923	0.891	−0.704
PW	9	1.50-2.50	0.889	1.991±0.115	0.346±0.082	17.878±4.214	0.361	−1.272
AW	9	1.55-2.40	0.786	1.972±0.092	0.276±0.065	14.397±3.393	0.276	−0.814
L/PW	9	1.02-1.43	–	1.152±0.039	0.116±0.027	10.305±2.429	2.031	5.291
M_3								
L	3	2.25-2.80	–	2.567±0.164	0.284±0.116	12.000±4.899	–	–
PW	3	1.70-1.90	−0.095	1.790±0.059	0.101±0.041	6.142±2.508	–	–
AW	3	1.80-2.06	0.603	1.920±0.076	0.131±0.054	7.400±3.021	–	–
L/PW	3	1.27-1.65	–	1.438±0.111	0.192±0.078	14.436±5.894	–	–
M^1								
L	1	2.42	–	–	–	–	–	–
W	1	3.41	–	–	–	–	–	–
M^2								
L	1	2.45	–	–	–	–	–	–
W	1	4.13	–	–	–	–	–	–
M^3								
L	1	1.42	–	–	–	–	–	–
W	1	2.50	–	–	–	–	–	–

Type. AMNH 5010, left mandible fragment with P_4-M_2, from "lower beds" of the Bridger Formation, near Ham's Fork, Bridger Basin Wyoming.

Hypodigm. The type and YPM 11999, 12000, 13228-2, 13230-1, 13232, 13233, and 14657 from various lower Bridger localities.

Geographical and Temporal Distribution. Early Bridgerian (early medial Eocene) of Wyoming.

Specific Diagnosis. As far as is known, *A. aemulus* differs from *A. westi* primarily in its smaller (about 30-40%) size.

Dental Formula. $I\frac{1,2}{1,2}$; $C\frac{1}{1}$; $P^{?},\frac{3,4}{3,4}$; $M\frac{1,2,3}{1,2,3}$.

Discussion. In his 1958 revision Gazin remarked that as far as he could determine *A. aemulus* was represented only by the type specimen. He then described this species on the basis of the holotype as follows (p. 75), "It may be noted, possibly in further characterizing the species, that the cusps of the lower molars are much subdued and the enamel is smooth." In his diagnosis of the then newly erected *Anaptomorphus wortmani* Gazin stated the following (p. 76): "Smaller than *Anaptomorphus aemulus*, closer in size to *Washakius insignis*. Lower molars relatively broader than in *A. aemulus*, cusps of trigonids a little better defined, paraconid more lin-

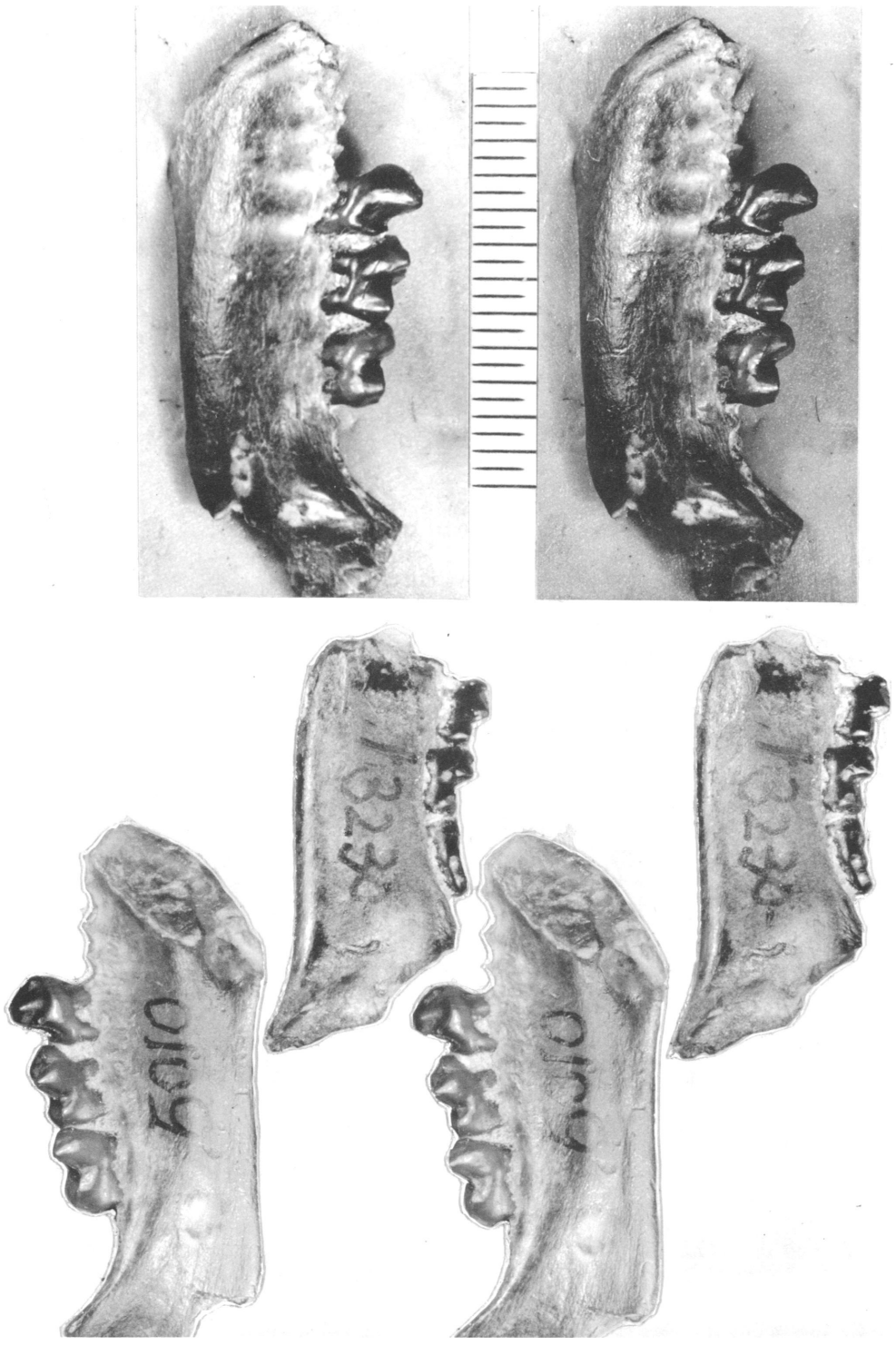


FIG. 10. *Anaptomorphus aemulus*, AMNH 5010, type, left P_4-M_2 (above and below left), and YPM 13230-1, right M_1-M_3 (below right), both from lower Bridger beds. Stereophotographs: above lateral and below medial views. Subdivisions on scale represent 0.5 mm.

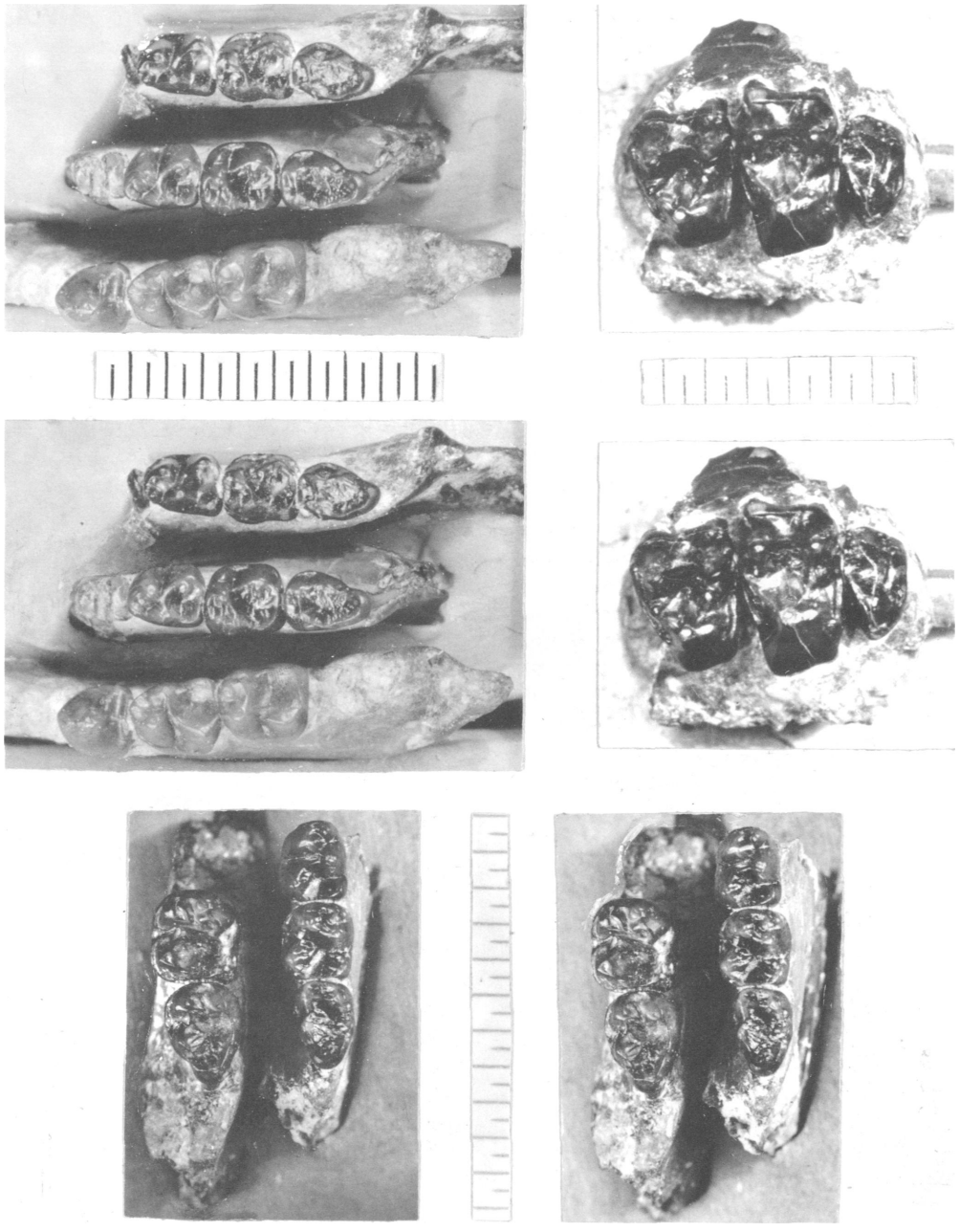


FIG. 11. *Anaptomorphus aemulus*, YPM 13230-1, right M_1-M_3 (above, left top); YPM 13233, type of "*A. wortmani*," right M_1-M_3 (above left center); AMNH 5010, type, left P_4-M_2 (above left bottom). *Anaptomorphus westi*, FM 15661, lower Bridger beds, right M^1-M^3 (above right). *Anaptomorphus* sp., UW 1540, left M_2-M_3 (below left), and UW 1475, left M_1-M_3 (below right), all from lower Bridger beds. Stereophotographs: all occlusal views. Subdivisions on scale represent 0.5 mm.

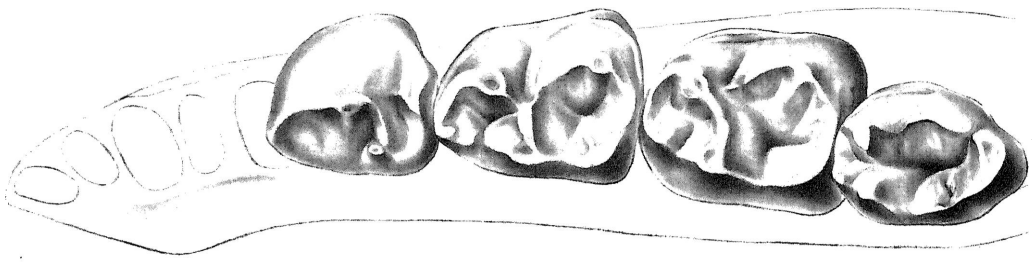


FIG. 12. *Anaptomorphus westi*, right horizontal ramus with P_4-M_3, based on FM 15041, type, and 15684, Bridgerian of Wyoming; occlusal view. Scale represents 1 mm.

gual and talonid basins slightly rugose." His discussion of this species, essentially a defense of its validity, was as follows (p. 76): "*Anaptomorphus wortmani* appears to be a valid species, but the difference in size from *A. aemulus* is not particularly great. Nevertheless, the four lower jaws (one more than Wortman saw) in the Marsh collection, all have teeth very close to the same size, distinctly and consistently smaller than in *A. aemulus*. Actually the length of the first two molars in *A. aemulus* is only about 17 percent greater than in the largest of the *A. wortmani* jaws and about 20 percent greater than in the smallest. However, somewhat smaller size, together with the relatively wider molars, somewhat more prominent and lingually placed paracone, and slight rugosity of the talonid basins would appear to warrant recognition of a distinct species. It should be noted, moreover, that the rugosity, so clearly evident in the type, and in the jaw figured by Wortman (Y.P.M. No. 13230-1), is not observed in the talonid basins of the more worn teeth of No. 13232. The horizon of the Bridger represented by the type specimen is not known, but accompanying one of the referred jaws, Y.P.M. No. 13228-2, there is a specimen label that reads 'Black's Fork,' so that its presence in the lower Bridger is verified."

I find the morphological distinctions between the type of *A. aemulus* and the artificial separation of "*A. wortmani*" unconvincing arguments for species separation. As stated above, a t-test between these failed to produce significant figures.

Anaptomorphus westi, new species
Figures 9, 11-14; Tables 3, 4

Type. FM 15041, right mandible fragment with M_{1-3}, collected from lower Bridger beds, Hawk locality of West (1973), SE¼ sect. 7, T 29 N, R 105 W, Wyoming.

Hypodigm. The type, and FM 15717 from Hawk loc.; FM 15661 and 15684, from Fault loc.; FM 15735 and 15739, Tree Road loc.

Geographical and Temporal Distribution. Early Bridgerian (early medial Eocene) of Wyoming.

Specific Diagnosis. About 30-40 percent larger in its known dental dimensions than *A. aemulus*.

Dental Formula. $I\frac{1,2}{1,2}$; $C\frac{1}{1}$; $P^{?}\frac{3,4}{3,4}$; $M\frac{1,2,3}{1,2,3}$.

Discussion. Recently recovered specimens of undoubted *Anaptomorphus* from the early Bridgerian Big Sandy Fauna (UW 1475 and 1540) and from the lower Bridger Fault, Hawk and Tree Road localities (West, 1969, 1970) strongly suggest that *Anaptomorphus* from these localities was distinctly larger than the known AMNH and YPM specimens.

FM 15684 from the Fault locality preserves P_4-M_1 and the alveoli anterior to P_4. The only possible distinction other than size, of dubious taxonomic significance on one specimen alone, is the slightly more extensive paracristid in the Fault specimen compared with that in the holotype of *A. aemulus*. There is little doubt, however, that *A. westi* is a valid species of the genus. The t-tests (discussed under the genus) show significant differences between the generotype and

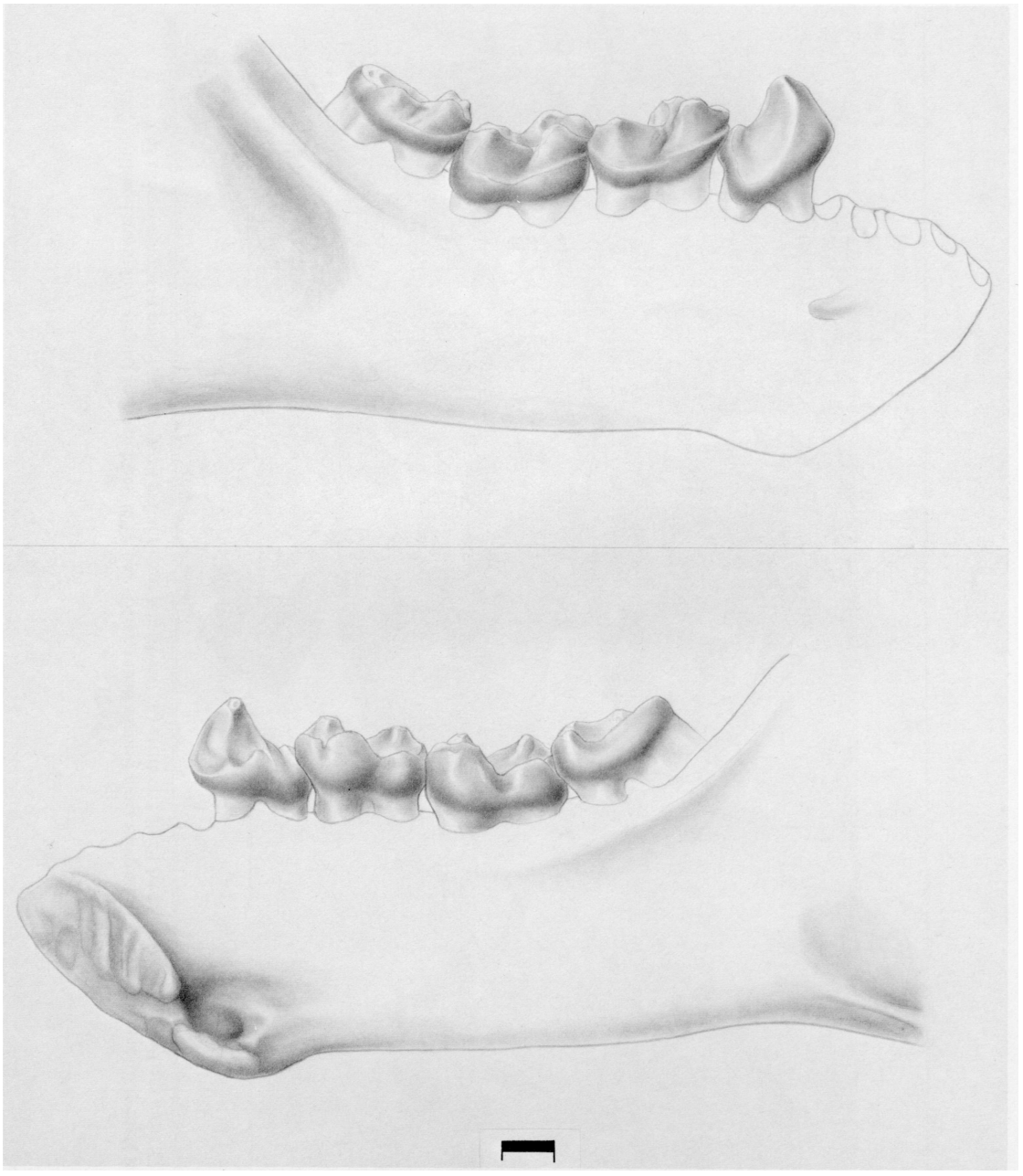


FIG. 13. *Anaptomorphus westi*, right horizontal ramus with P_4-M_3, based on FM 15041, type, and 15684, Bridgerian of Wyoming; lateral (above) and medial (below) views, respectively. Scale represents 1 mm.

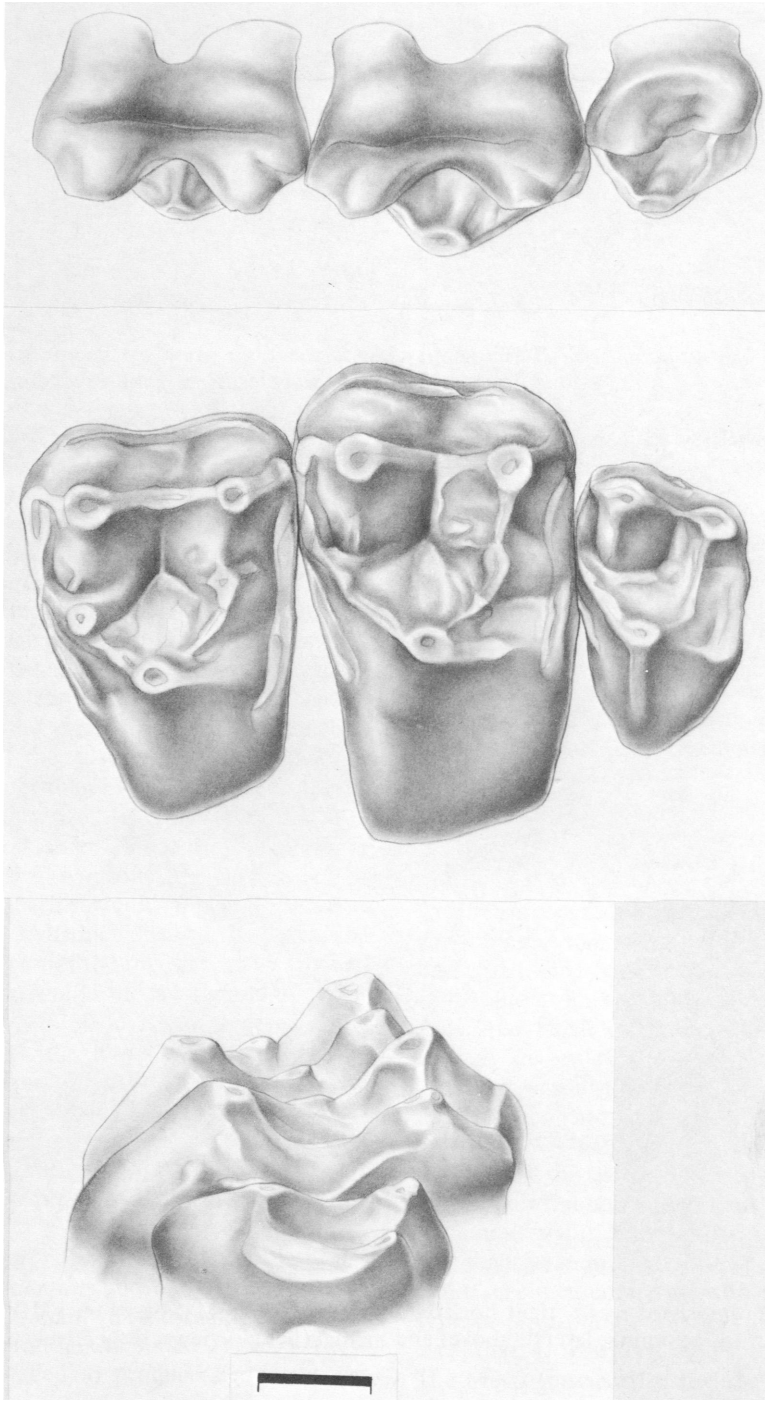


FIG. 14. *Anaptomorphus westi*, left M^{1-3}, based on FM 15661, Bridgerian of Wyoming; buccal (above), occlusal (middle), and distal (below) views, respectively. Scale represents 1 mm.

TABLE 4

Numerical Data of Specimens of *Anaptomorphus* from Bridger Beds (AMNH and YPM Specimens) of Largely Unknown Locality (*A. aemulus*); from the Hawk, Tree Road, and Fault Localities (*A. westi*); and from the Big Sandy Local Fauna (*Anaptomorphus* sp.)

	M^1		M^2		M^3		P_4		M_1			M_2			M_3		
	L	AW	L	AW	L	AW	L	PW	L	PW	AW	L	PW	AW	L	PW	AW
AMNH 5010, type	–	–	–	–	–	–	2.00	2.00	2.30	2.00	1.90	2.25	2.00	2.00	–	–	–
YPM 13233, type of *A. wortmani*	–	–	–	–	–	–	–	–	2.10	1.65	1.50	2.15	1.50	1.55	–	–	–
YPM 11999	–	–	–	–	–	–	–	–	1.95	1.70	1.60	–	–	–	–	–	–
YPM 12000	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.25	–	1.60
YPM 13230-1	–	–	–	–	–	–	–	–	2.10	1.65	1.50	2.00	1.75	1.80	2.20	–	1.50
YPM 13232	–	–	–	–	–	–	–	–	2.10	1.65	1.50	2.15	1.50	1.55	–	–	–
YPM 14657	–	–	–	–	–	–	–	–	2.10	1.70	1.60	2.05	1.85	1.85	–	–	–
N	–	–	–	–	–	–	1	1	6	6	6	5	5	5	2	–	2
OR	–	–	–	–	–	–	–	–	1.95-2.30	1.65-2.00	1.50-1.90	2.00-2.25	1.50-2.00	1.55-2.00	2.20-2.25	–	1.50-1.60
M	–	–	–	–	–	–	–	–	2.18	1.72	1.60	2.12	1.72	1.75	2.22	–	1.55
FM 15041	–	–	–	–	–	–	–	–	2.75	2.4	2.05	2.75	2.55	2.44	2.75	1.84	2.00
FM 15661	2.42	3.41	2.45	4.13	1.42	2.50	–	–	–	–	–	–	–	–	–	–	–
FM 15684	–	–	–	–	–	–	2.55	2.35	2.73	2.26	2.13	–	–	–	–	–	–
FM 15717	–	–	–	–	–	–	–	–	2.95	2.52	2.22	–	–	–	–	–	–
FM 15735	–	–	–	–	–	–	–	–	2.70	2.3	2.15	–	–	–	–	–	–
FM 15739	–	–	–	–	–	–	–	–	–	–	–	2.65	2.50	2.50	3.25	–	–
N	1	1	1	1	1	1	1	1	4	4	4	2	2	2	2	1	1
OR	–	–	–	–	–	–	–	–	2.70-2.95	2.26-2.52	2.05-2.22	2.65-2.75	2.50-2.55	2.44-2.50	2.75-3.25	–	–
M	–	–	–	–	–	–	–	–	2.78	2.37	4.27	2.70	2.52	2.47	3.00	–	–
UW 1475	–	–	–	–	–	–	–	–	2.15	1.76	1.70	2.02	1.77	1.80	2.25	1.77	1.80
UW 1540	–	–	–	–	–	–	–	–	–	–	–	2.40	2.35	2.40	2.65	1.90	2.06
N	–	–	–	–	–	–	–	–	1	1	1	2	2	2	2	2	2
OR	–	–	–	–	–	–	–	–	–	–	–	2.02-2.40	1.77-2.35	1.80-2.40	2.25-2.65	1.77-1.90	1.80-2.06

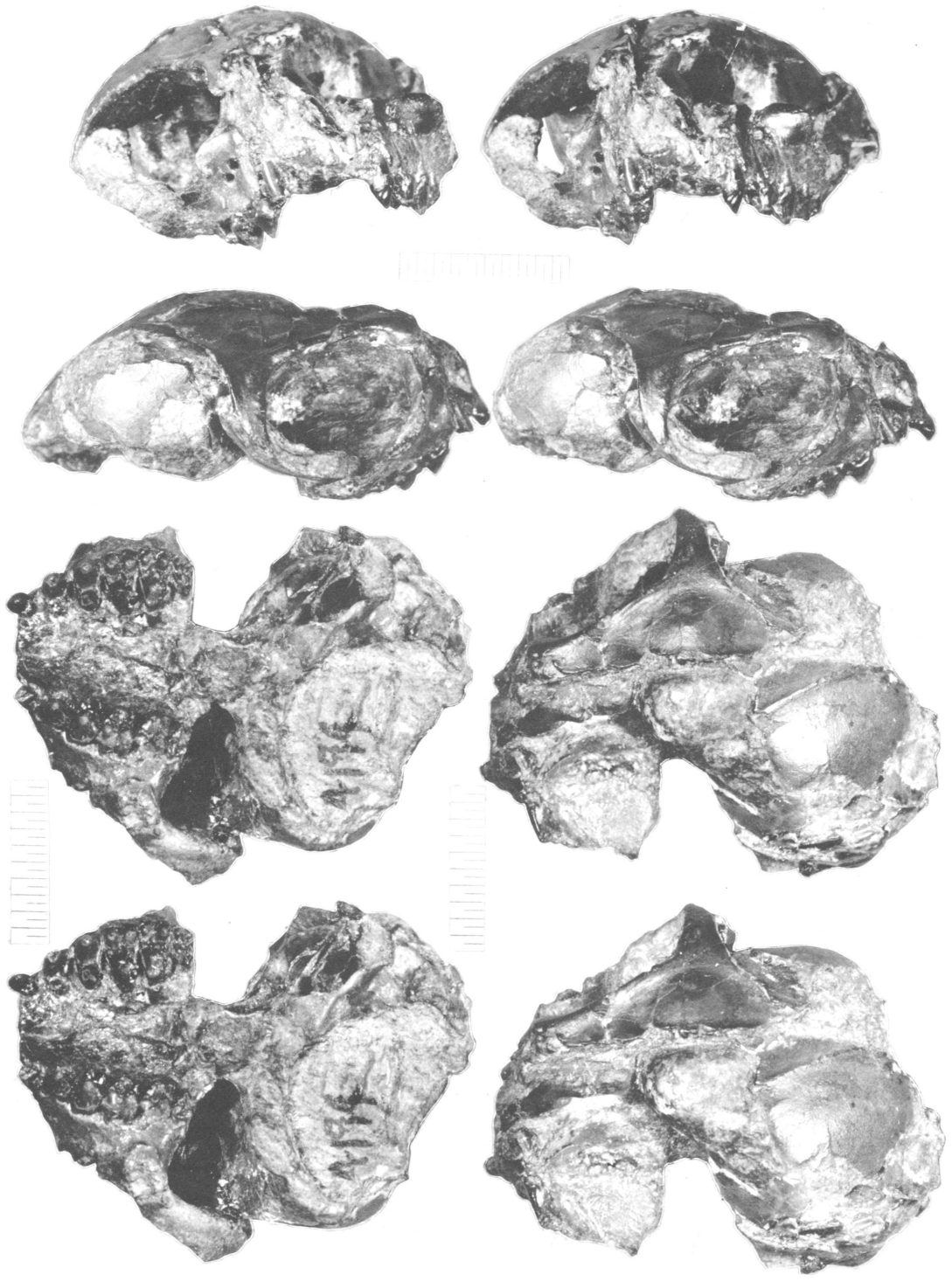


FIG. 15. *Tetonius homunculus*, AMNH 4194, type, lower Gray Bull beds, crushed cranium. Stereophotographs: frontal (above), lateral (middle), ventral (below left), and dorsal (below right) views, respectively. Subdivisions on scale represent 0.5 mm.

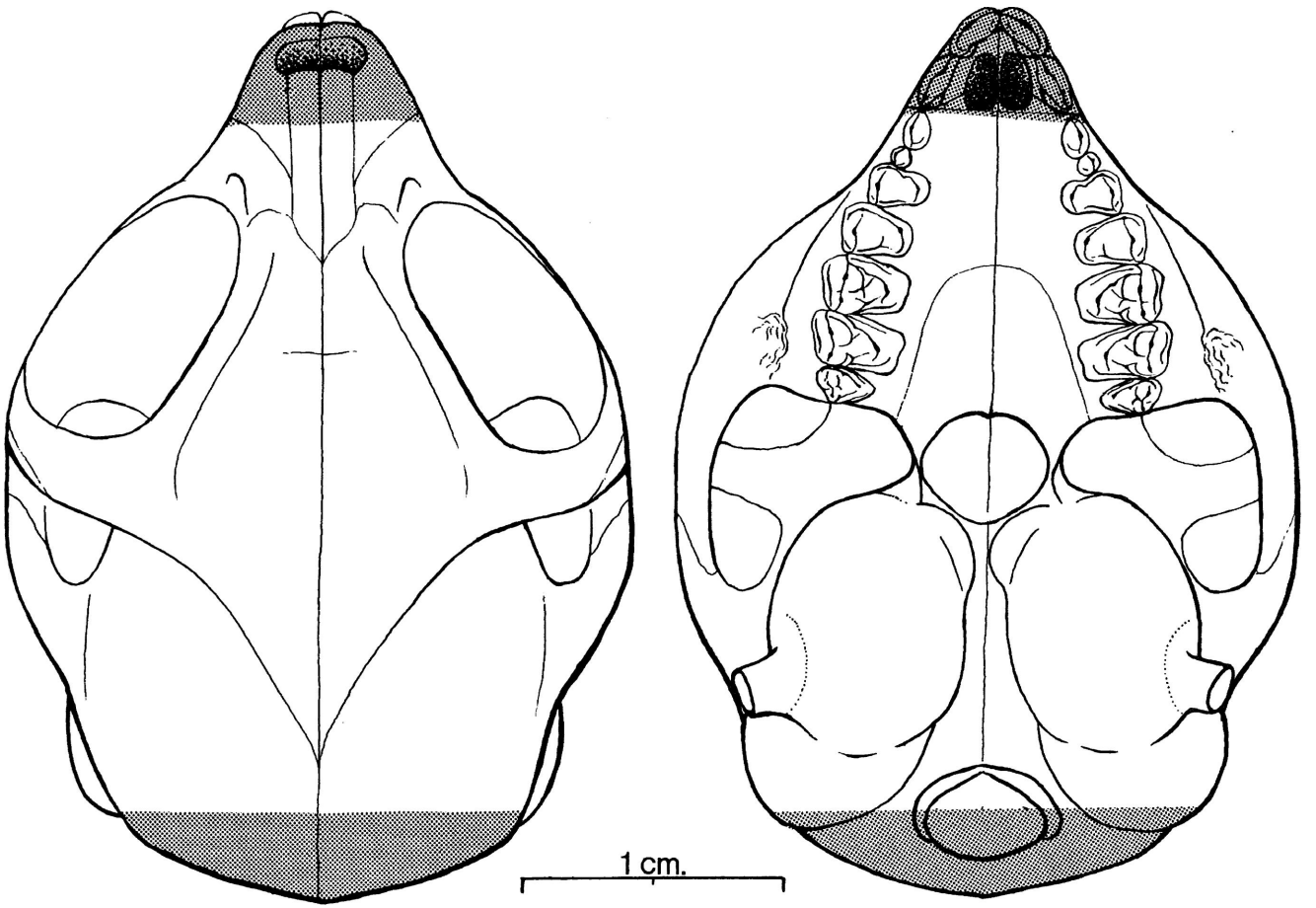


FIG. 16. *Tetonius homunculus*, cranium based on AMNH 4194, type, crushed skull, and AMNH 88887, isolated anterior teeth, Wasatchian of Wyoming and Colorado; dorsal (left) and ventral (right) views, respectively. Reconstruction shown by uniform stippling and broken lines.

A. westi. I interpret these to be of species rank size differences rather than a mere sample difference of the same species.

Etymology. For Dr. Robert M. West, the collector of the type and hypodigm, in recognition of his work on the Eocene vertebrate faunas of southwestern Wyoming.

SUBTRIBE TETONIINA ABEL, 1931

Tetoniidae Abel, 1931, p. 199.

Type Genus. Tetonius Matthew, 1915.

Included Taxa. Type genus, and *Anemorhysis* Gazin, 1958, *Absarokius* Matthew, 1915, and *Mckennamorphus*, new genus.

Subtribe Diagnosis. Anaptomorphinines with an enlarged first incisor, relatively small canines, and reduced third molars, which share a more recent common ancestor with each other than with any other anaptomorphinines.

Discussion. Other than the character complex cited, no additional features help to convincingly diagnose this subtribe.

TETONIUS MATTHEW, 1915

Anaptomorphus: Cope, 1882, p. 152.
Tetonius Matthew, 1915, p. 459.
Paratetonius Seton, 1940, p. 39.
?*Tetonoides*: Robinson, 1967, p. 187.

Type Species. Tetonius homunculus (Cope, 1882).

Included Species. Type species, *Tetonius*? *ambiguus* (Matthew, 1915), and probably an additional unnamed species.

Geographical and Temporal Distribution. Early Wasatchian (earliest Eocene) of Wyoming and Colorado.

Generic Diagnosis. Anaptomorphines with premolariform fourth premolars which lack distinct paraconids and metaconids, or have minimal development of these; the lower fourth premolar is higher crowned than any of the other premolars or molars. They are distinct from *Anemorhysis* in having a $P\frac{4}{4}$ taller and more robust and molar cingulids less well developed than those of the latter. The major difference of this genus from *Absarokius* lies in the relatively lower and less robust $P\frac{4}{4}$.

Discussion. As far as it is known *Tetonius* is restricted to the early Wasatchian and its most abundant species is *Tetonius homunculus.* The discussions under *T. homunculus* and *Absarokius* are particularly pertinent to the generic diagnosis.

Adaptations. The dentition shows a combination of features which is so far unique in the family. On all specimens known to me the tooth rows are tightly packed. No diastemata appear and the teeth overlap and crowd one another. The median pair of lower incisors is enlarged, bear low crowns, heavy cingulids, and when the two are viewed together, it is apparent that they formed a robust device, each with a long cutting edge running from the apex to the distal extremity of the crown. It is unlikely that this pair of teeth was used as an awl-like tool. Their long apical edge suggests uses such as fruit procuring, peeling, or any activity involving extensive incisal handling.

I have selected (fig. 19) several isolated teeth from specimens collected at East Alheit Pocket, some of which I judge to be upper incisors (AMNH 88887). The allocations are clearly tenuous, yet I believe that they are of sufficiently high probability to warrant comment. The upper central pair of incisors are long, mesiodistally broad, yet buccolingually constricted, with prominent mesiodistal cutting edges. They are basally wide in all directions and have a distinct lingual cingulum. What I judge to be I^2 has a distal, vertically oriented, sharp cutting edge, with a small, basal, distally oriented prominence.

The enlarged lower tooth has a robust root and, in terms of relative size and surface area, it is the most important element of the antemolar dentition, along with the equally relatively prominent P_4. In effect these two teeth appear to be the two most distinctive segments of the dentition of the genus. Both the incisors and the canine are characterized by being transversely broad, probably a derived condition for the anaptomorphines. Both P_3 and P_4 have a distolingually enlarged talonid.

The most distinctive character of the lower molars is the basal inflation of the trigonid cusps and the shallowness of the talonid basin. Except on M_1, the paraconid is closely twinned with the metaconid, and the paracristid extends more mesially than the paraconid, forming a low, but

apparently important, cingulid. M_3 is reduced, although the relatively longer talonid of this tooth suggests derivation from an ancestry in which M_3 was relatively larger and longer than those of the molars anterior to it.

M^1 is distinctly less transverse than M^2, and M^3 is much smaller than M^1. The molar hypocone is an anomalous thickening of the postcingulum. In addition to the hypocone there is a well-developed protocone fold. Lingual fusion of the pre-cingula and postcingula occurs in many specimens.

The two halves of the mandible are relatively uncurved anteriorly. The lower jaw was more or less V-shaped, and the symphysis was almost certainly unfused. The symphysis is relatively very large, however, with a superior and inferior transverse torus and, as in most other omomyids, a distinct canal associated with some of the tongue muscle. No specimen shows the ascending ramus.

The molar roots of *Tetonius homunculus* are of some interest. As a very large number of isolated teeth are known from East Alheit Pocket the root structure could be studied in detail. The most significant feature appears to be the extent of roots under the crowns. The lingual root is particularly massive and its "apex" (i.e., the part farthest from the crown) is flared out and very broad. Both mesially and distally the root extends buccally, whereas between them a deep furrow can be usually found, the extensions substantially adding perhaps to the surface area of the root. The centrally facing surfaces of both buccal roots of the upper molars also have a broad furrow, and similarly the roots of the lower molars are broadly furrowed on the sides facing the transverse midline of the tooth. It appears that the furrows are the result of increase in root size.

Comparisons with isolated molars of *Omomys carteri* clearly show differences in both root construction and some aspects of crown morphology (fig. 25). The trigon and talonid basins of *Omomys carteri* are significantly and consistently deeper than those of *Tetonius homunculus*. I see a causal correlation between the basin morphology and the extent and shape of root structure. The deeper basins and the consequently higher crests surrounding them suggest more extensive, orthal cutting in *Omomys*. On the other hand the surprisingly shallow basins of *Tetonius homunculus* and the lower and relatively thicker based crests hint that masticatory movements were relatively more mesiolingual than those in *Omomys carteri*. The more robust root patterns of *Tetonius homunculus* appear to reflect that in this species buttressing was better developed to resist the more transversely directed forces than those in *Omomys carteri*.

Enlarged incisors of the particular kind described, slightly enlarged fourth premolars, and slightly reduced $M\frac{3}{3}$ suggest reduction of molar function in favor of incisor and premolar use. Enlarged incisors and reduced molar teeth are usually associated with highly omnivorous, partly frugivorous taxa (*Pan*, *Pithecia*, *Chiropotes*, and *Cacajao*), and, short of a detailed analysis of occlusion and wear, this might be the best interim hypothesis for the diet of *Tetonius homunculus*.

Tetonius homunculus (Cope, 1882)
Figures 15-26, 28, 29, 142; Table 5

Anaptomorphus homunculus Cope, 1882, p. 152.
Tetonius homunculus (Cope 1882) Matthew 1915, p. 459.
Paratetonius steini Seton 1940, p. 39.
?*Tetonoides* sp. Robinson, 1967, p. 187.

Type. AMNH 4194, crushed skull with C-M^3 preserved, from Gray Bull beds, Willwood Formation, Big Horn Basin, Wyoming.

Hypodigm. The type, and AMNH 59619, 59634, 59671, 80051, 80075-80078, 80083, 80084, 80086, 80090, 80093, 80099, 80951, 80952, UCMP 44159, 44290, 44934, 59414 from East Alheit Pocket, Wasatch Formation, Colorado; AMNH 80038, 80039, 80052, UCMP 46195, 46196, 59422, 59423 from Timberlake Quarry, Wasatch Formation, Colorado; AMNH 80037, UCM 28854, 28944, 28958, UCMP 44768, 44769A-44769C, 44769E-44769J from Sand Quarry, Wasatch Formation, Colorado; AMNH 80060, UCMP 44029, 44052, 44054, 44055 from Despair Quarry, Wasatch Formation, Colorado; AMNH 41, 15062-15065, 15072, 15693, 16933, 16934, CM 12189, 12190, 12225, 12276, 12391, UCM 19389, YPM 23167,

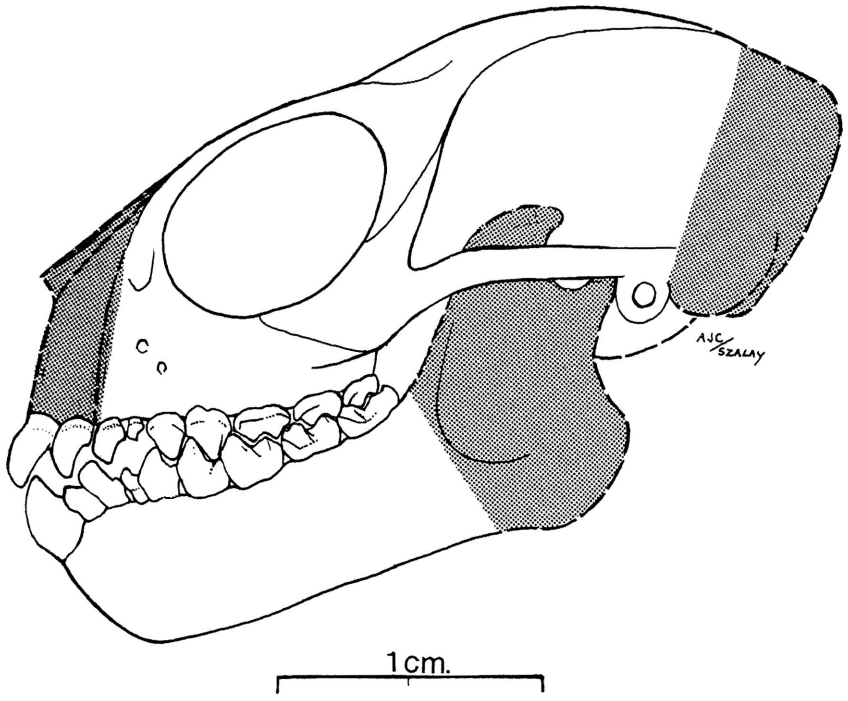


FIG. 17. *Tetonius homunculus*, reconstructed cranium and mandible, based on AMNH 4194, crushed skull, CM 12190, left mandibular ramus with I_1-M_3, and AMNH 88887, isolated teeth, Wasatchian of Wyoming and Colorado; lateral view. Reconstruction shown by uniform stippling and broken lines.

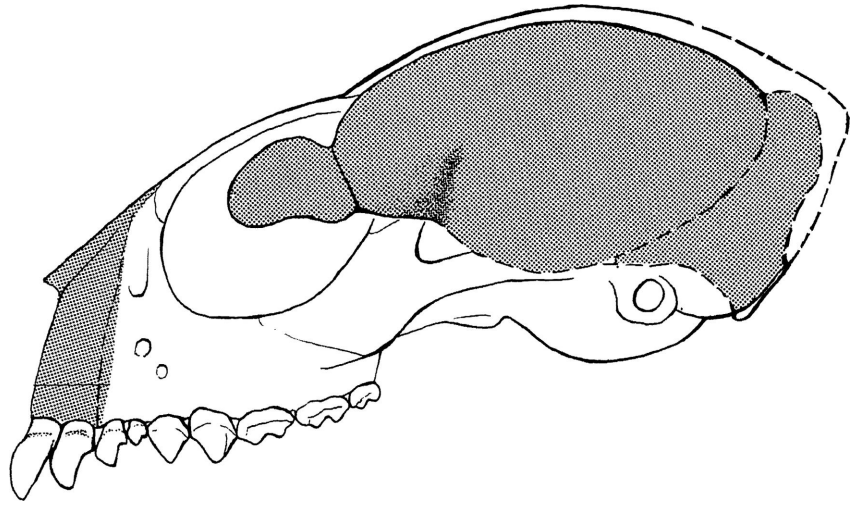


FIG. 18. *Tetonius homunculus*, lateral view of skull to show endocast, based on AMNH 4194, crushed skull, and AMNH 88887, isolated anterior teeth, Wasatchian of Wyoming and Colorado. Reconstruction shown by uniform stippling and broken lines.

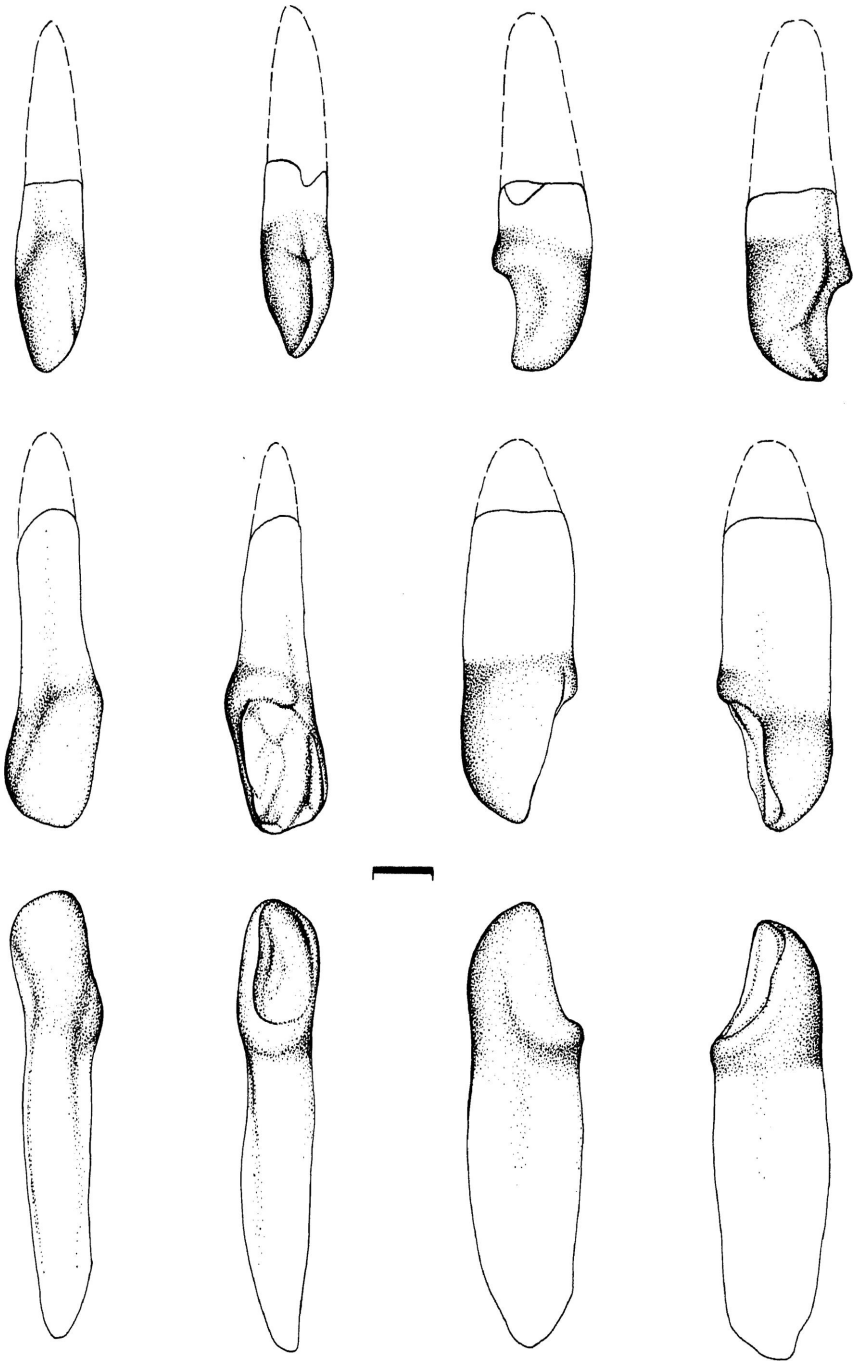


FIG. 19. *Tetonius homunculus*, AMNH 88887, isolated anterior teeth, East Alheit Pocket, Wasatch beds, right I^2 (above), left I^1 (middle), and left I_1 (below); from left to right: mesial, distal, buccal, and lingual views, respectively. Reconstruction shown by broken lines. Scale represents 1 mm.

TABLE 5
Numerical Data for Specimens of *Tetonius homunculus* from Gray Bull Beds and Wasatch Beds of the Four Mile Localities

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P^3								
L	3	1.95-2.00	–	1.967±0.017	0.029±0.012	1.590±0.649	–	–
PW	3	2.40-2.60	0.277	2.517±0.060	0.104±0.042	4.480±1.829	–	–
L/AW	3	0.75-0.81	–	0.782±0.018	0.031±0.013	4.335±1.770	–	–
P^4								
L	6	1.85-2.00	–	1.942±0.027	0.066±0.019	3.565±1.029	−0.326	−2.254
PW	6	2.40-3.00	0.621	2.825±0.096	0.236±0.068	8.706±2.513	−1.393	1.739
L/AW	6	0.63-0.77	–	0.691±0.020	0.050±0.014	7.497±2.164	0.856	0.029
M^1								
L	19	1.90-2.25	–	2.063±0.021	0.090±0.015	4.395±0.713	0.272	−0.335
PW	19	2.75-3.40	0.640	3.026±0.042	0.185±0.030	6.197±1.005	0.729	−0.088
L/AW	19	0.65-0.76	–	0.683±0.008	0.033±0.005	4.894±0.794	0.844	0.424
M^2								
L	26	1.40-2.15	–	1.879±0.025	0.130±0.018	6.972±0.967	−1.680	7.302
PW	26	3.10-3.75	0.451	3.283±0.031	0.157±0.022	4.842±0.672	1.437	2.070
L/AW	26	0.43-0.64	–	0.573±0.007	0.037±0.005	6.516±0.904	−2.113	8.506
M^3								
L	11	1.10-1.35	–	1.218±0.024	0.078±0.017	6.577±1.402	0.213	−0.984
AW	11	2.00-2.35	0.525	2.155±0.036	0.119±0.025	5.662±1.207	−0.077	−1.057
L/AW	11	0.51-0.63	–	0.566±0.010	0.033±0.007	5.958±1.270	0.093	−0.257
I_3								
L	1	1.35	–	–	–	–	–	–
PW	1	1.20	–	–	–	–	–	–
L/PW	1	1.12	–	–	–	–	–	–
C								
L	1	1.50	–	–	–	–	–	–
PW	1	1.30	–	–	–	–	–	–
L/PW	1	1.15	–	–	–	–	–	–
P_2								
L	1	0.60	–	–	–	–	–	–
PW	1	0.87	–	–	–	–	–	–
L/PW	1	0.69	–	–	–	–	–	–
P_3								
L	14	1.25-1.90	–	1.584±0.047	0.178±0.034	11.409±2.156	−0.372	−0.055
PW	14	1.25-1.60	−0.115	1.386±0.032	0.122±0.023	8.930±1.688	0.313	−1.230
L/PW	14	0.83-1.52	–	1.153±0.047	0.175±0.033	15.448±2.919	0.336	0.424
P_4								
L	26	1.70-2.15	–	1.896±0.025	0.128±0.018	6.806±0.944	0.241	−0.664
PW	26	1.40-2.00	0.520	1.723±0.029	0.147±0.020	8.621±1.195	0.027	0.169
L/PW	26	0.99-1.26	–	1.105±0.017	0.085±0.012	7.746±1.074	0.111	−1.497
M_1								
L	36	1.90-2.35	–	2.131±0.017	0.101±0.012	4.769±0.562	−0.293	−0.180
PW	36	1.60-2.35	0.445	1.924±0.026	0.155±0.018	8.121±0.957	0.101	0.472
AW	36	1.50-1.95	0.481	1.747±0.021	0.123±0.015	7.094±0.836	−0.454	−0.477
L/PW	36	0.94-1.26	–	1.113±0.014	0.082±0.010	7.392±0.871	0.197	−0.712

TABLE 5—(*Continued*)

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
M_2								
L	37	1.75-2.25	–	2.078±0.017	0.101±0.012	4.895±0.569	−0.947	1.843
PW	37	1.60-2.10	0.416	1.897±0.021	0.128±0.015	6.772±0.787	−0.343	−0.507
AW	37	1.70-2.15	0.293	1.942±0.021	0.128±0.015	6.623±0.770	−0.062	−0.748
L/PW	37	0.95-1.31	–	1.099±0.012	0.074±0.009	6.745±0.784	0.565	0.978
M_3								
L	2	2.10-2.25	–	–	–	–	–	–
PW	2	1.30-1.35	–	–	–	–	–	–
AW	2	1.40-1.60	–	–	–	–	–	–
L/PW	2	1.62-1.67	–	–	–	–	–	–

23169, 23174, 23181-23185, 23187, 23189, 23568, 23618, MCZ 3516 from Gray Bull beds, Willwood Formation, Big Horn Basin, Wyoming.

Geographical and Temporal Distribution. Early Wasatchian (earliest Eocene) of Wyoming and Colorado.

Specific Diagnosis. Differs from *T.? ambiguus* in having a less robust first lower incisor.

Dental Formula. $I\frac{1,2}{1,2}; C\frac{1}{1}; P\frac{2,3,4}{(2),3,4}; M\frac{1,2,3}{1,2,3}$.

Discussion. The systematic treatment of *T. homunculus* has been relatively uncomplicated except for the naming of "*Paratetonius steini*" by Seton, its recognition by Gazin (1952), and by some queried references of *T. homunculus* specimens. Seton's (1940) diagnostic differences of "*Paratetonius steini*" from *T. homunculus* become meaningless when the specimen is compared to either the Colorado Wasatch or Wyoming Willwood samples.

The type cranium of *Tetonius homunculus*, found by Wortman in 1881, first figured by Cope (1884), and subsequently reconstructed by Matthew (1915), and AMNH 41, also found by Wortman in 1891, have been the bases for the controversy concerning the dental formula of *T. homunculus*. The last reviewer of the genus and species was Matthew (1915) who has established that the type skull showed the presence of a canine, a short diastema dorsal to it, and P^3-M^3. Based particularly on AMNH 41 and 15063, and on the indirect evidence offered by the type specimen of *T.? ambiguus* (AMNH 15072) Matthew concluded correctly (although not for AMNH 15072) that there was a tiny P_2 anterior to P_3. Because of the poor sample available to him, however, he considered the large anterior tooth a canine, unable to perceive on the basis then known that there were two additional alveoli mesial to the P_2 alveolus and distal to the large alveolus at the front of the jaw. This view, which suggested the loss of four anterior teeth in the lower jaw of *Tetonius* (i.e., loss of three incisors, and the first premolar), as opposed to two (one incisor and P_1), as presented here, has been the underlying assumption by workers dealing with this genus directly or indirectly (Kelly and Wood, 1954; Morris, 1954; McKenna, 1960; Robinson, 1967).

From the same level and locality as the type skull (Matthew, 1915, p. 460, but see ambiguous remark by Wortman, 1904, p. 212) comes AMNH 41, left and right upper cheek teeth (P^3-M^3) and a mature left mandible fragment with P_3-M_3. These specimens are the original hypodigm of the taxon *Tetonius homunculus* (Cope, 1882). An additional important specimen is CM 12190 from the Gray Bull beds (locality S 10-11 of the Carnegie Museum). It is most similar of all known *Tetonius* in the detailed morphology of the teeth, in the robustness and depth of the mandible, and in the proportions of the teeth to those of AMNH 41. Although Robinson (1967) has assigned this specimen to *?Tetonoides* sp., it is clearly *Tetonius homunculus*. In addition to the full complement of molars, two incisors, and canine CM 12190 has three premolars. Scrutiny of AMNH 41 reveals that the proportion of the preserved cheek teeth to those of the mandible and a small depression anterior to P_3 on the anterior part of the jaw point to the presence of a P_2, is as in CM 12190.

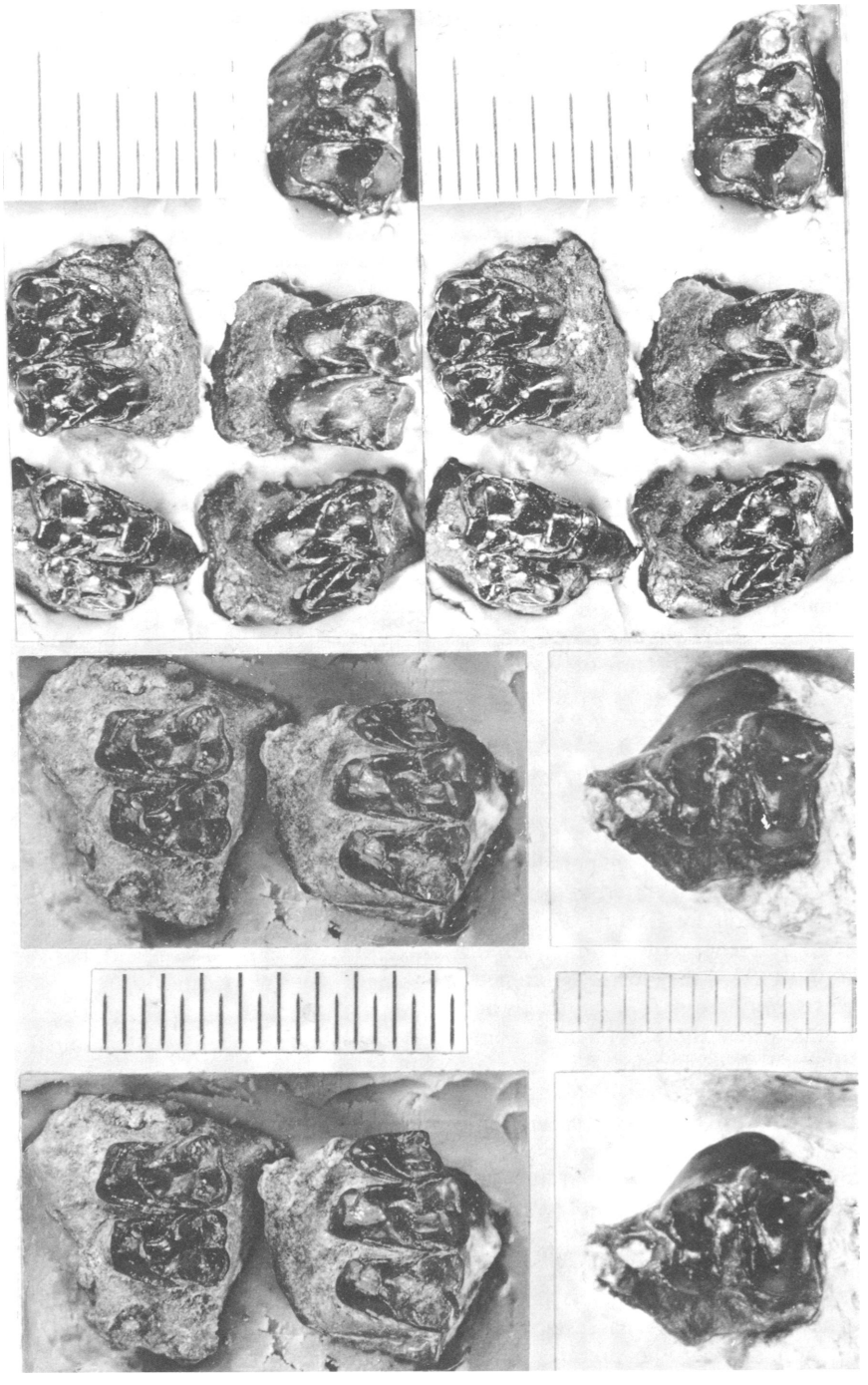


FIG. 20. *Tetonius homunculus*, AMNH 88825, left P^{3-4}; AMNH 88826, right M^{1-2}; AMNH 88827, right M^{2-3}; AMNH 88828, left M^{1-2}; and AMNH 88829, left M^{2-3} (above), all from East Alheit Pocket, Wasatch beds; YPM 23568, right M^{1-2} (below left); AMNH 15062, Gray Bull beds, right M^{1-3} (below middle); AMNH 88806, East Alheit Pocket, Wasatch beds, left C and P^2 alveoli and P^{3-4} (below right). Stereophotographs: occlusal views. Subdivisions on scales represent 0.5 mm.

FIG. 21. *Tetonius homunculus*, AMNH 88803, nine M_1s (above), AMNH 88804, 10 M_2s (middle), and AMNH 88805, 10 M_3s (below), all from East Alheit Pocket, Wasatch beds. Stereophotographs: occlusal views. Subdivisions on scales represent 0.5 mm.

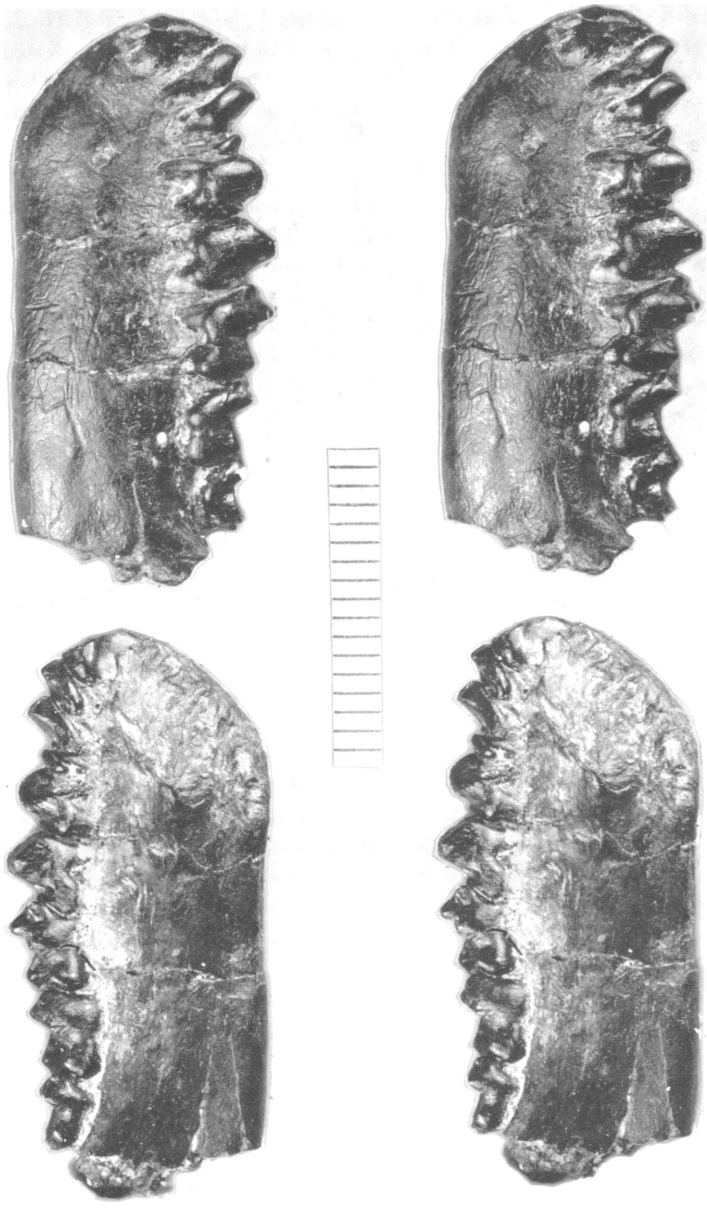


FIG. 22. *Tetonius homunculus*, CM 12190, Gray Bull beds, left mandibular ramus with I_1-M_3. Stereophotographs: above lateral and below medial views. Subdivisions on scale represent 0.5 mm.

Alveoli of P_2 or the teeth themselves are known in other specimens allocated to *T. homunculus*. These specimens (YPM 23167 and AMNH 88888, fig. 26), from Gray Bull and Wasatch beds, do not seem to differ in either quantitative or qualitative features (other than the presence of P_2) from other known samples of *T. homunculus*. Although most known lower jaws of

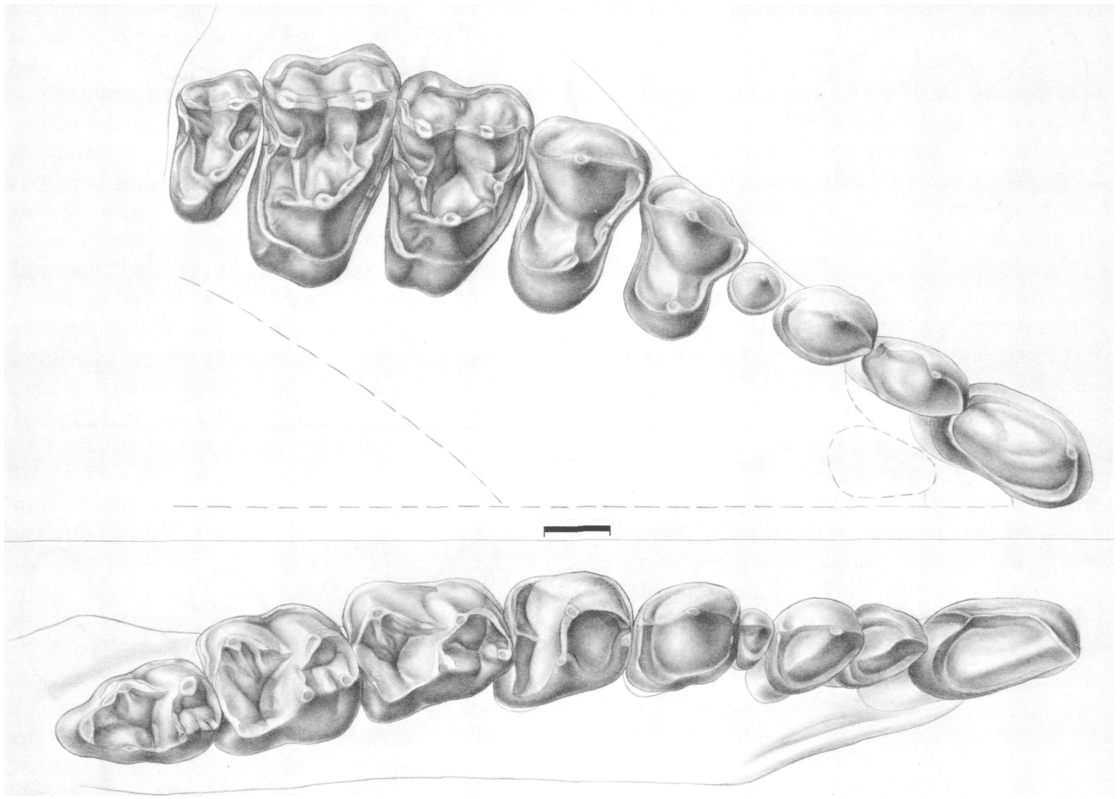


FIG. 23. *Tetonius homunculus*, composite upper and lower dentition, based on AMNH 4194, type, AMNH 88887, CM 12190, and numerous maxilla and mandibular fragments, Wasatchian of Wyoming and Colorado; occlusal views. Reconstruction shown by broken lines. Scale represents 1 mm.

the East Alheit *T. homunculus* sample lack P_2, the presence of P^2 alveolus in a maxilla fragment with P^3 and P^4 (AMNH 88806) that can be referred with a high degree of probability to *T. homunculus*, suggests that individuals with P_2 were present in the East Alheit population.

Quite obviously the size and shape of P_2 and the teeth anterior and posterior to it are interrelated. Although P_3 is a two-rooted tooth, there are mandible fragments allocated to *T. homunculus* (YPM 23183) that have single-rooted, anteroposteriorly constricted, third lower premolars. It appears that probable selection for shorter (or smaller?) mandibles resulted in the reduction (P_2) and shortening (P_3) of the anterior premolar dentition.

The presence or absence of an upper or lower second premolar and the single- or double-rooted nature of the third lower premolar have been used extensively (e.g., Gazin, 1952, 1958) to discriminate taxonomically between the various samples of omomyids, particularly those of *Tetonius*. The unusually large samples of *Tetonius* from McKenna's (1960) Four Mile quarries, particularly from East Alheit Pocket, have been decisive in determining the importance of this feature. Although clearly the presence or absence of a reduced tooth can be useful in generic or specific assignments, the use of such a feature must be tempered by considering the size of the sample from one locality, the morphology of all other teeth and mandibular structure, symphyseal construction, particularly as it is correlated with the robustness of the anterior dentition, and

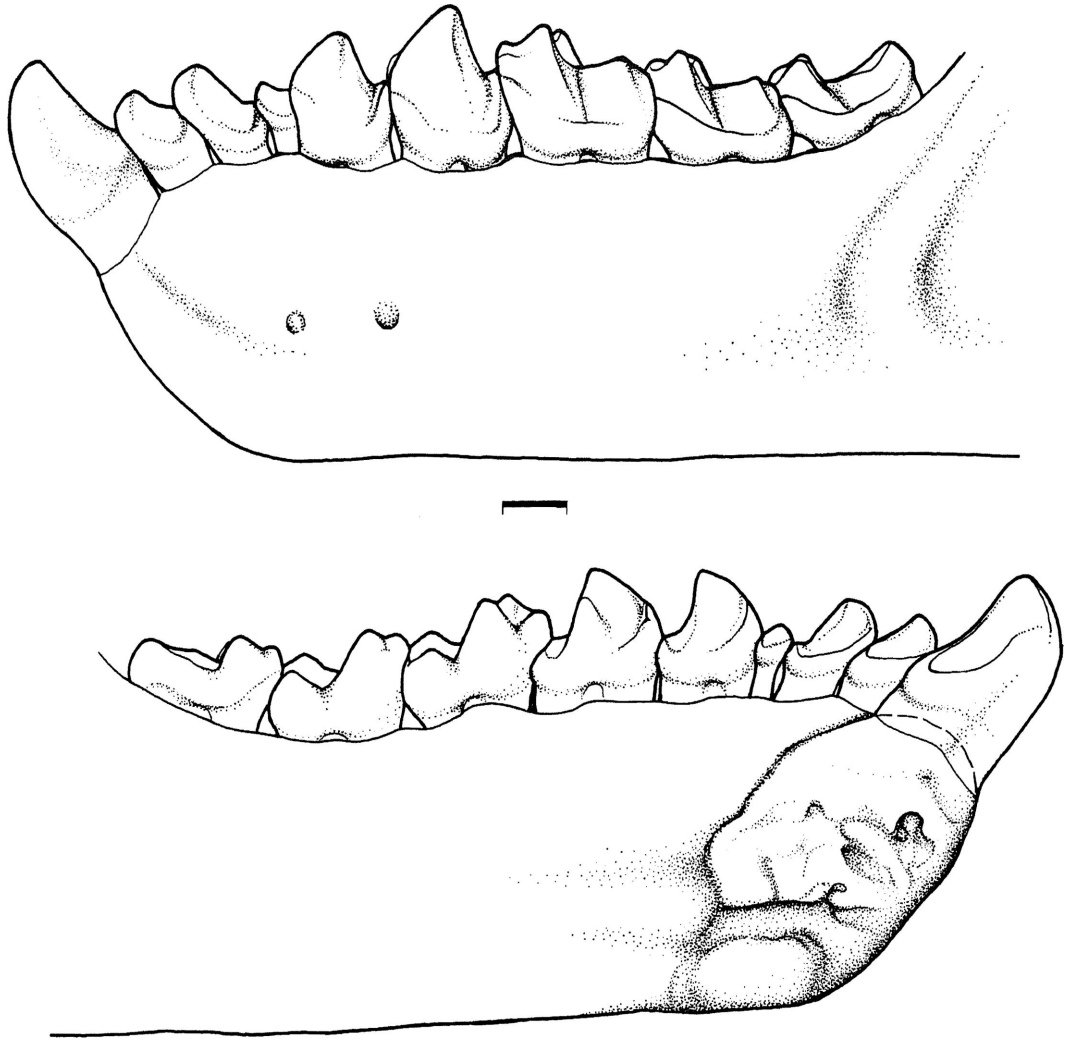


FIG. 24. *Tetonius homunculus*, left horizontal ramus with complete dentition, based on CM 12190, Wasatchian of Wyoming and Colorado; lateral (above) and medial (below) views. Scale represents 1 mm.

the proportions of the various antemolar units such as the incisors, canine, and the premolars to the molars. Most often, however, use of the presence or absence of the tiny second premolars as a supraspecific taxonomic character has been disproportionate to its inferred biological significance.

On the basis of the morphology and size the abundant, larger Four Mile anaptomorphine is inseparable on the species level from *Tetanius homunculus*. It is in this sample that the presence or absence of the second premolar is a variable feature. Although the majority of the mandibles lack P_2, AMNH 59619, from East Alheit Pocket preserves a P_2 alveolus, and the only two maxilla fragments (AMNH 88806 and 88825, fig. 20) with P^3-P^4 and alveoli anterior to them preserve both the canine and the small P^2 alveoli, suggesting the presence of a lower counterpart in these specimens. Another specimen from Yale loc. 87

from Gray Bull beds, YPM 23167, also retains a P_2 alveolus; based on the morphology of P_3-M_1 it can be clearly allocated to *Tetonius homunculus*.

Cleaning the area distal to the root of the canine on the right side of the type skull revealed the faintest traces of a mesiodistally constricted root, presumably that of P^2. This, however, cannot be established with sufficient certainty because of the extremely poor preservation of the bone on the type. Were there no P^2 in *Tetonius homunculus*, it would then be the only tarsiiform, extant or extinct, with a large diastema between the most anterior premolar and the canine. The moderate size of P_3 in *T. homunculus* makes it unlikely that maxillae of this species had a diastema between P^3 and the upper canine. When P^2 was lost, the gap between these teeth most likely was closed. The high coefficient of variation, 11.4, for the length of P_3 indicates that the presence or absence of P_2 and the consequent length of P_3 were more variable than other dental parameters of this species.

A large lower Gray Bull sample with the anterior dentition is needed to finally characterize the limits of variation in the presence or absence of P_2 in *T. homunculus*. It seems reasonable to me not to use this probably variable feature as a species distinction between *T. homunculus* and a nearly equal sized, unnamed species of *Tetonius*, known so far from the Four Mile localities.

McKenna (1960, p. 74) pointed out that the type specimen of Seton's (1940) *Paratetonius steini*, MCZ 3516, right lower (P_4-M_3) and left upper (P^3-M^3) jaw fragments, can be referred to *Tetonius homunculus* without any doubt. In addition, Gazin (1962, p. 34), in conjunction with his remarks on "*Anemorhysis sublettensis*" briefly stated that, "Following description of *Anemorhysis sublettensis* . . . as a possible form of *Paratetonius*, it was realized that the type of *Paratetonius, P. steini*, was not distinct from *Tetonius homunculus*."

Tetonius? *ambiguus* (Matthew, 1915)
Figures 26-28

Tetonius ambiguus Matthew, 1915, p. 462.

Type. AMNH 15072, left mandible fragment with broken large incisor, alveoli for small incisor and canine, and P_3-M_2. Collected from lower Gray Bull beds, Willwood Formation, Big Horn Basin, Wyoming.

Hypodigm. Type only.

Geographical and Temporal Distribution. Early Wasatchian (earliest Eocene) of Wyoming.

Specific Diagnosis. P_3 appears to be relatively smaller than P_4 compared with any known specimens of *T. homunculus*. If this taxon is valid, it has a more robust lower first incisor than the latter.

Discussion. Little can be said of the poorly preserved type specimen, the only representative of this taxon. I believe that the molar size differences from *T. homunculus* cited by Matthew (1915, p. 462) are due to the fact that the teeth in this specimen were etched and heavily worn before burial. This specimen has a P_3 similar to that of the highly derived *Mckennamorphus despairensis*. Whether this is significant or not in terms of generic allocation I could not decide, the sample being so poor.

The possibility exists that AMNH 15064 from the lower Gray Bull beds ("Lower Forks Dorsey Creek") is *T.*? *ambiguus*, a suggestion based on the rather diminutive P_3 of that specimen.

Tetonius sp.
Figure 29

cf. *Anemorhysis minutus*: McKenna, 1960, p. 65.
Anemorhysis musculus: Guthrie, 1967, p. 17.
Tetonius musculus: Delson, 1971, p. 338.

Discussion. This sample, which includes specimens UCMP 46192, 47159, and 46194 from East Alheit Pocket, now referred to either as a species distinct from or a possible artificial small and gracile sample of *T. homunculus*, was, along with other specimens, allocated to cf. *Anemorhysis minutus* (Loomis, 1906) by McKenna (1960).

The differences in the morphology of P_4 between species of *Tetonius* and *Anemorhysis* are treated under the generic discussion. However, it may be noted again that the referred P_4s of *Anemorhysis tenuiculus* have well-developed metaconids and paraconids and are approximately equal in height to the first molar trigonid. In species of *Tetonius* the fourth lower premolar is robust, lacks a well-defined metaconid and paraconid, and is taller than the first molar trigonid.

Thus, species differences between referred

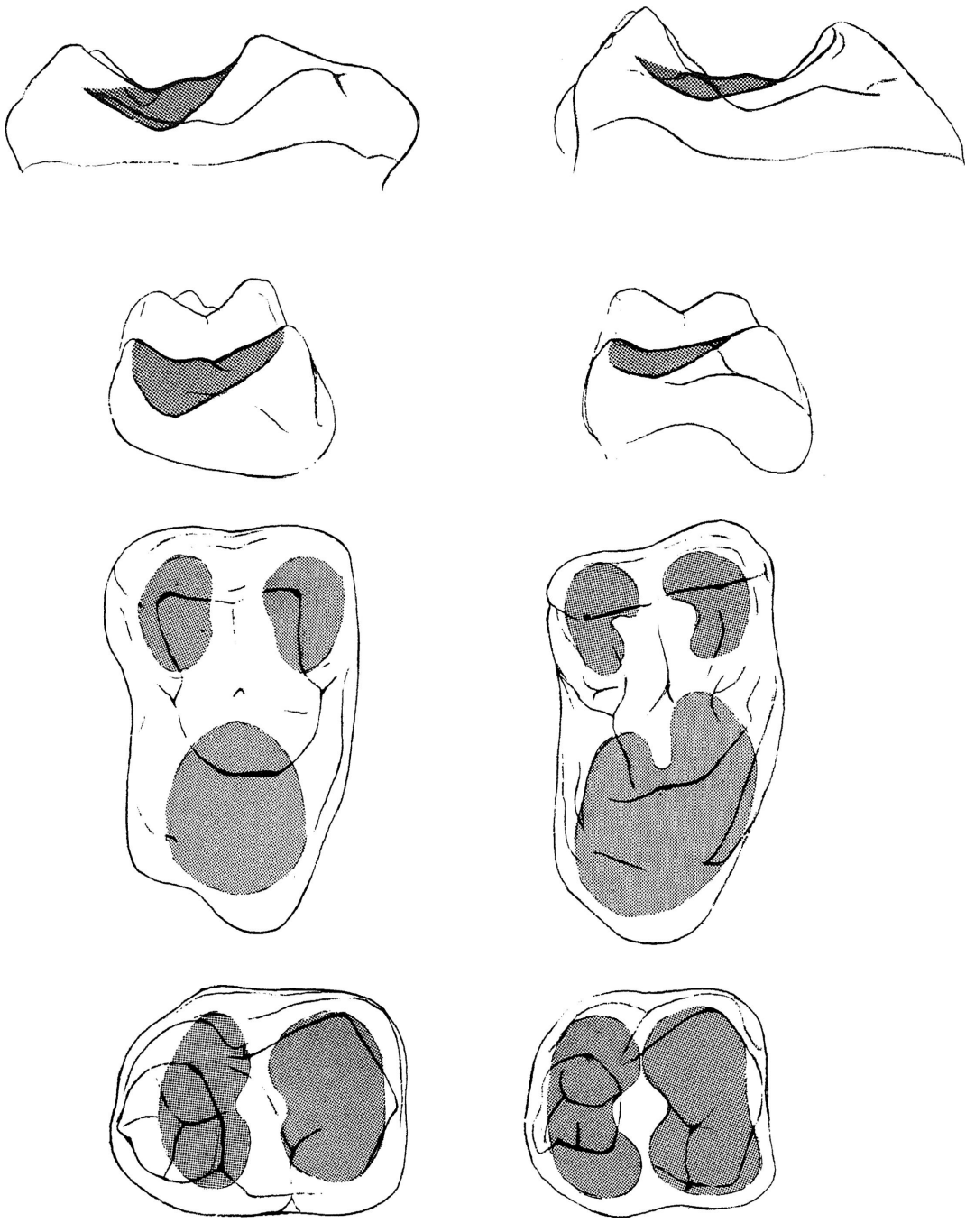


FIG. 25. Comparison between upper and lower molars of *Tetonius* sp. (right, based on isolated molars from East Alheit Pocket) and *Omomys* sp. (left, CM 6398 and 8747). The stippled areas of the top four figures show the depth of the trigon and trigonid basins from a distal view of the molars, whereas the lower four figures depict the basal configuration of the roots superimposed on the occlusal views. The most noticeable differences are the greater depth of the basins in *Omomys* and the somewhat more robust lingual root of *Tetonius*. The differences may be correlates of more orthal masticatory movements in *Omomys* compared to the more mesiolingual ones in *Tetonius*. The teeth of *Tetonius* appear to be better buttressed for the more medially directed stresses in mastication.

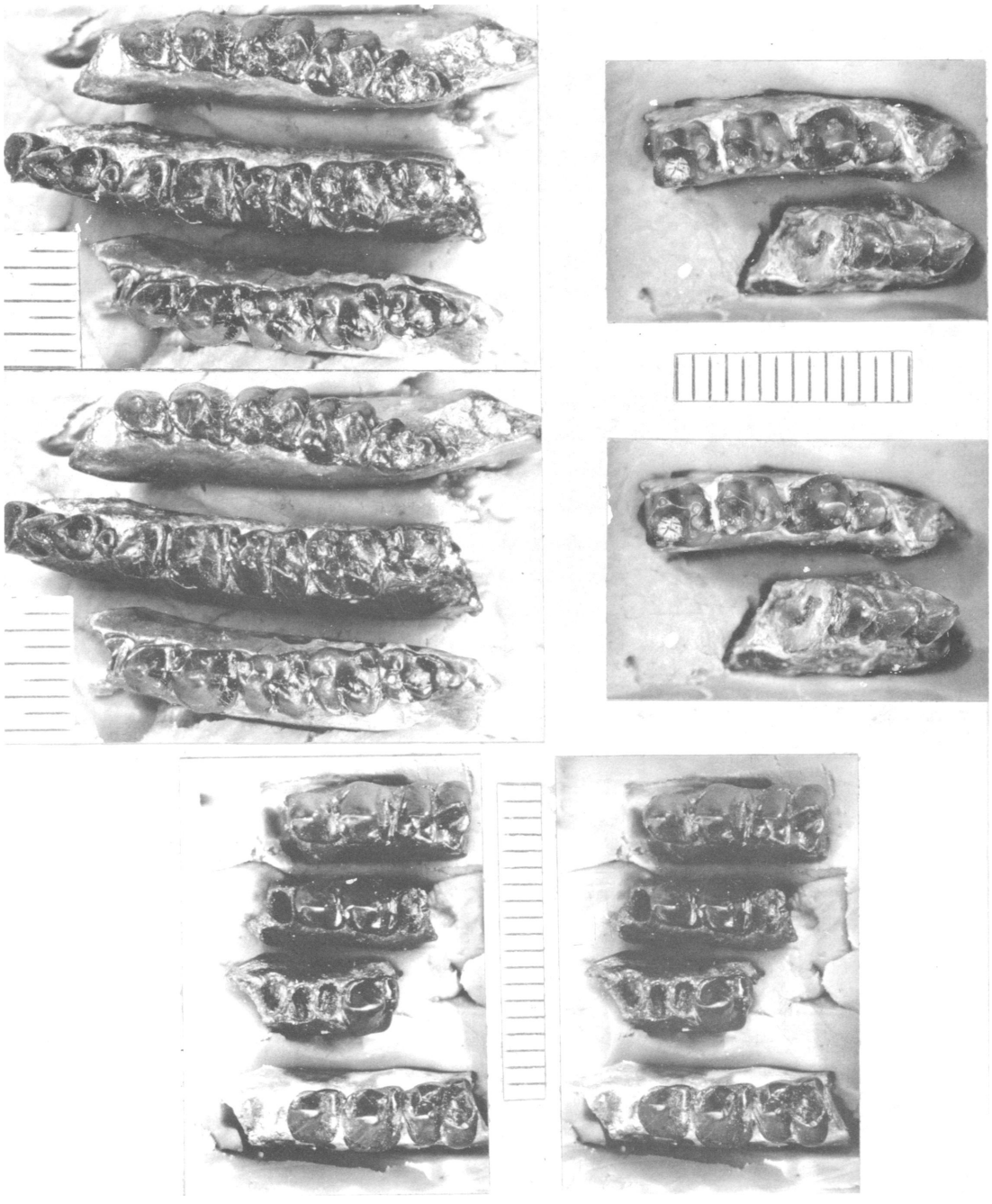


FIG. 26. *Tetonius homunculus*, AMNH 80086, East Alheit Pocket, Wasatch beds, right P_3-M_3 (left top); CM 12190, Gray Bull beds, left horizontal ramus with complete dentition (second row on left); AMNH 59619, East Alheit Pocket, left P_3-M_3 (third row on left); AMNH 88888, right P_3-M_1 (fourth row); AMNH 88889, right $P_{3\text{-}4}$ (fifth row); AMNH 88890, right P_4 (sixth row); all East Alheit Pocket; YPM 23167, Gray Bull beds, alveoli for C and P_2, P_3-M_1 (seventh row). *Tetonius*? *ambiguus*, AMNH 15072, type, Gray Bull beds, left root of I_1, P_3-M_2 (right top). *Mckennamorphus despairensis*, UCMP 44055, type, Despair Quarry, Wasatch beds, right I_2-P_3 and broken P_4 (second row right). Stereophotographs: occlusal views. Subdivisions on scales represent 0.5 mm.

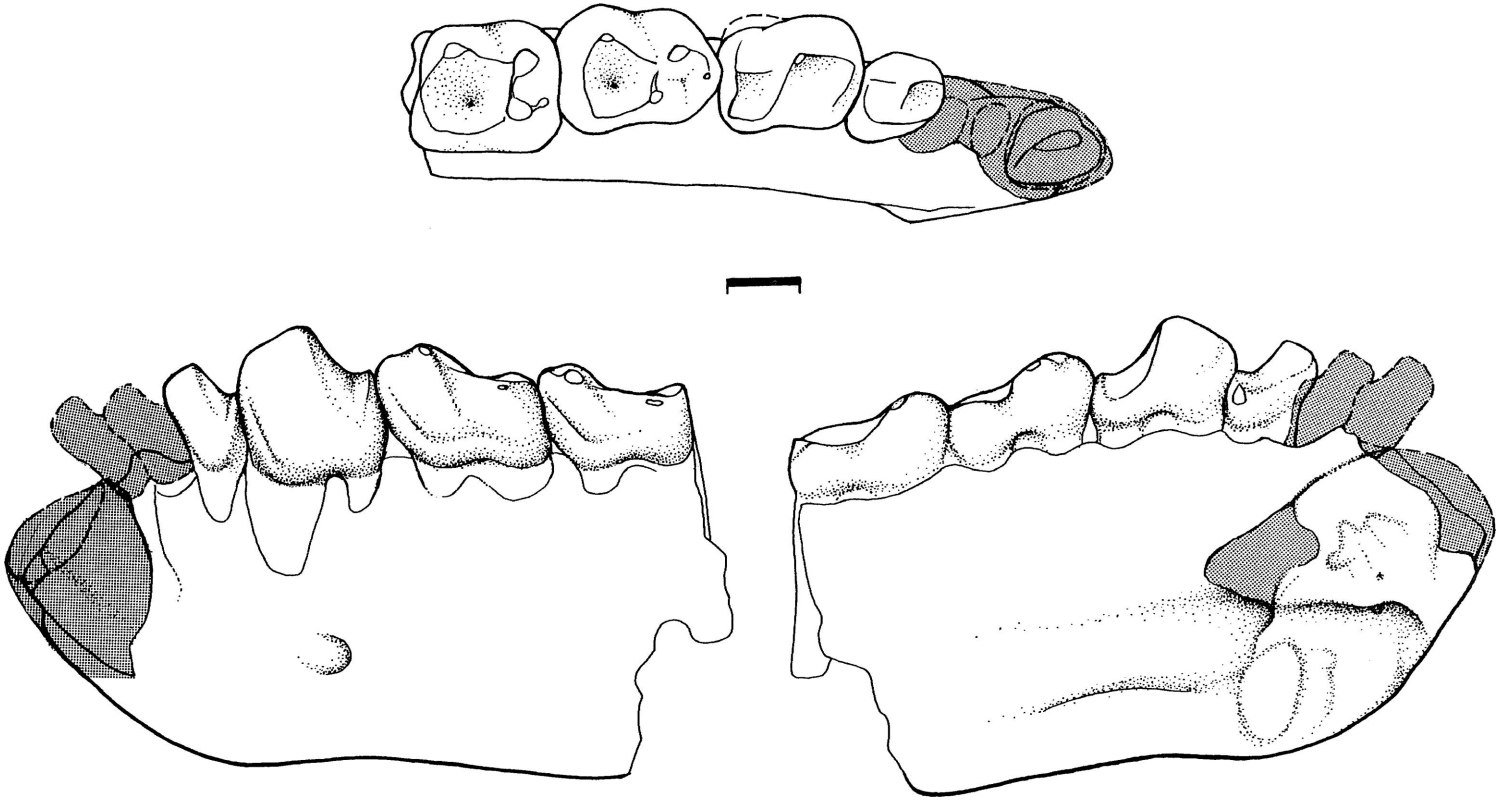


FIG. 27. *Tetonius*? *ambiguus*, right mandible fragment with P_3-M_2, based on AMNH 15072, type, Wasatchian, Wyoming; occlusal (above), lateral (below left), and medial (below right) views. Reconstruction shown by stippling and broken lines. Scale represents 1 mm.

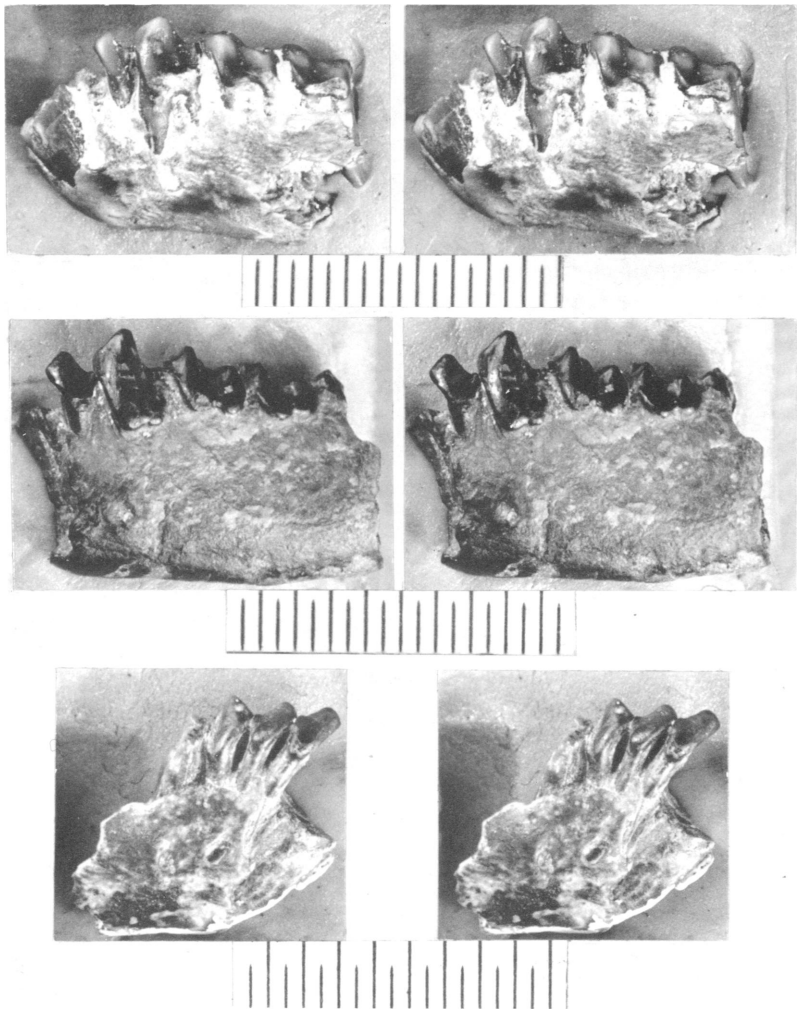


FIG. 28. *Tetonius*? *ambiguus*, AMNH 15072, type, Gray Bull beds, part of left I_1 and P_3-M_2 (above). *T. homunculus*?, AMNH 15064, Gray Bull beds, left P_3-M_2 and broken M_3 (middle). *Mckennamorphus despairensis*, UCMP 44055, type, Despair Quarry, Wasatch beds, part of left I_1, I_2-P_3, and broken P_4 (below). Stereophotographs: lateral views. Subdivisions on scales represent 0.5 mm.

specimens of *Anemorhysis tenuiculus* that have a P_4 and *Tetonius* sp. from the Four Mile Quarries are shown primarily in the construction of this tooth. In addition, the proportions of the lower molars, shown by M_3 and the alveoli of the best-preserved mandible (AMNH 12830), indicate size and proportion differences between the lower dentitions of *Anemorhysis tenuiculus* and *A. musculus* on the one hand, and this unusual, but undoubted sample of *Tetonius* on the other.

ANEMORHYSIS GAZIN, 1958

Tetonius: Matthew, 1915, p. 463.
Anemorhysis Gazin, 1958, p. 25.
Uintalacus Gazin, 1958, p. 29.
Tetonoides Gazin, 1962, p. 34.

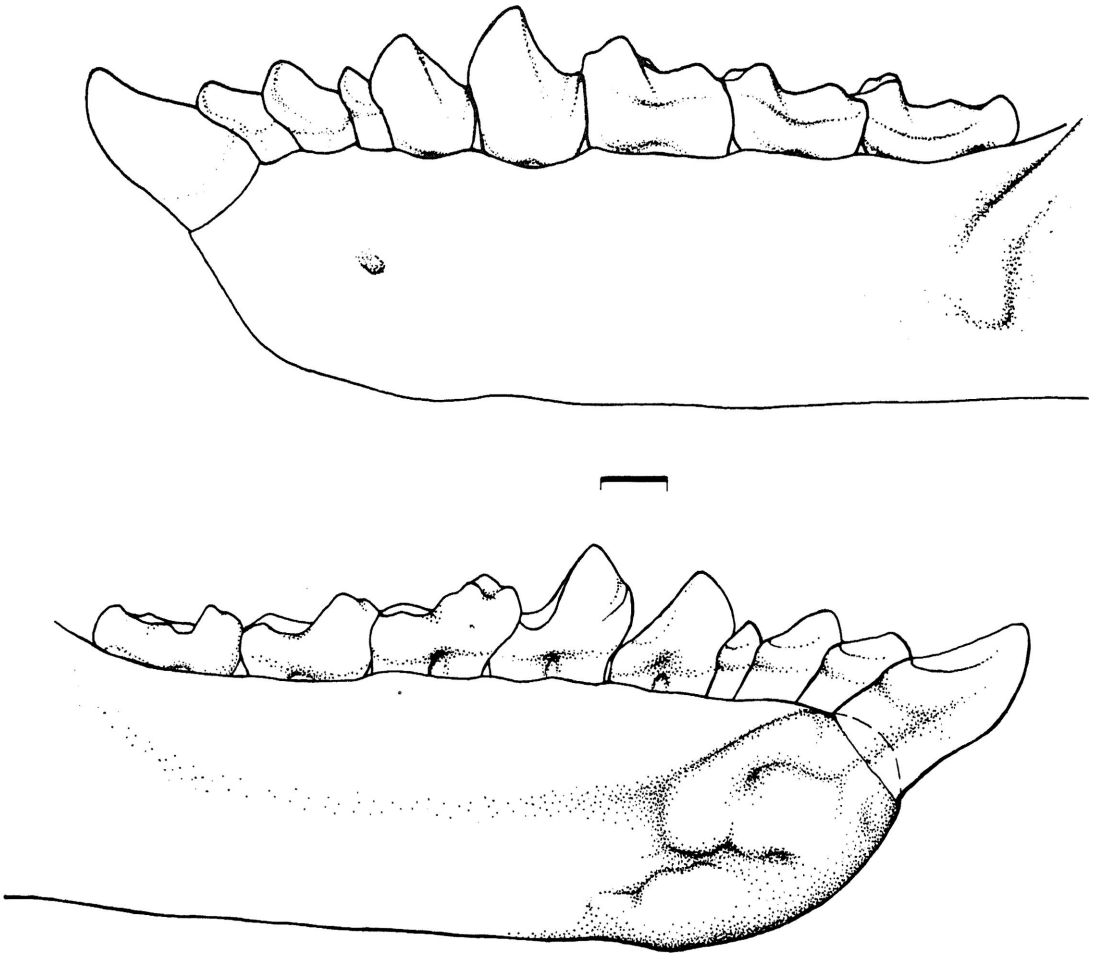


FIG. 29. *Tetonius* sp., left horizontal ramus with complete dentition (P_2 is reconstructed) representing either an unnamed species of *Tetonius* smaller than *T. homunculus* or possibly a small, gracile variant of *Tetonius homunculus*, based on UCMP 46192, East Alheit Pocket; lateral (above) and medial (below) views. Scale represents 1 mm.

Type Species. Anemorhysis sublettensis (Gazin, 1952).

Included Species. The type species, *Anemorhysis musculus* (Matthew, 1915), and *A. tenuiculus* (Jepsen, 1930).

Geographical and Temporal Distribution. Early to medial Wasatchian (early to medial early Eocene) of Wyoming.

Generic Diagnosis. Small anaptomorphines with semimolariform to premolariform fourth lower premolars, having distinct paraconids and metaconids that are lower or subequal to the height of the molars. Buccal cingulids of lower molars are distinct, more often better developed than those of *Tetonius*.

Discussion. One of the many difficult problems surrounding the numerous taxonomic concepts based on specimens now allocated to one of the three recognized species of this genus involves geographical and temporal variation.

The taxonomy of the very small early Eocene anaptomorphines represents a morass of names,

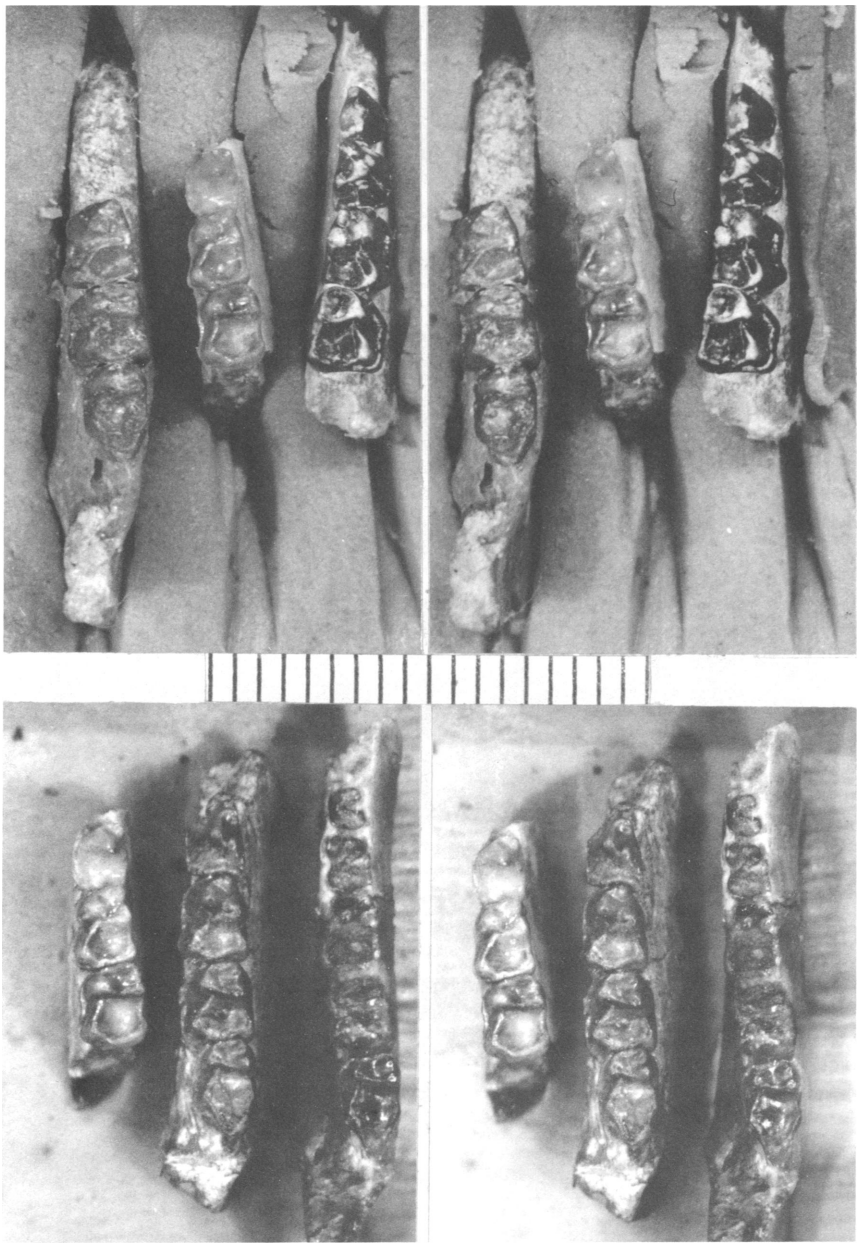


FIG. 30. Comparisons of representative lower dentition samples of *Anemorhysis* spp. *Above: from left to right*: PU 1723, Golden Valley beds, left M_{1-3} (*A. tenuiculus*); USNM 19205, type of *A. sublettensis*, Wasatch beds, upper Green River Basin, left P_4-M_2; and USNM 22426, type of "*Tetonoides pearcei*," lower Wasatch beds, Washakie Basin, right P_3-M_2 (*A. tenuiculus*). *Below*: USNM 19205, type of *A. sublettensis*, Wasatch beds, upper Green River Basin, left P_4-M_2; PU 17232, Golden Valley beds, left P_4-M_3 (*A. tenuiculus*); and AMNH 12830, type of *A. musculus*, Lysite beds, left M_3 and most of horizontal ramus with alveoli. Stereophotographs: occlusal views. Subdivisions on scale represent 0.5 mm.

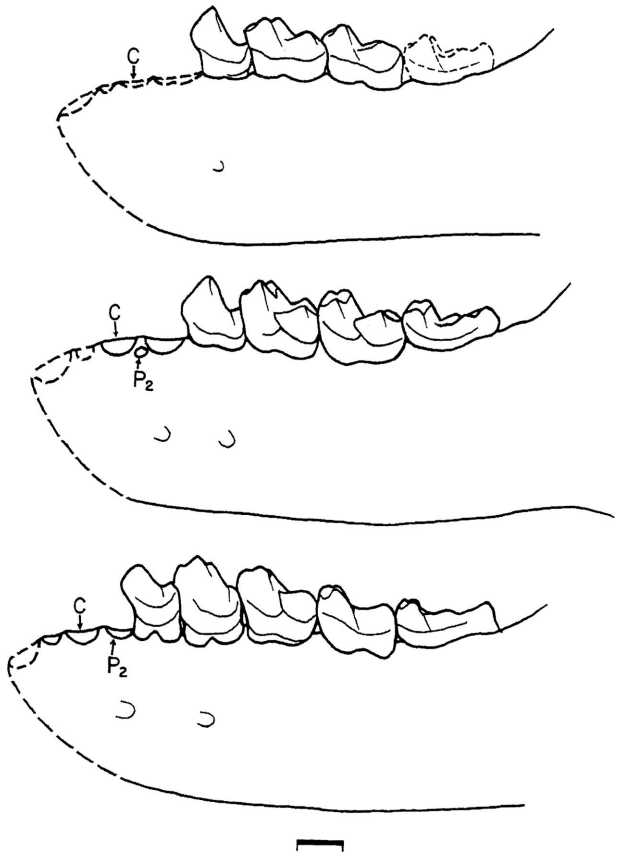
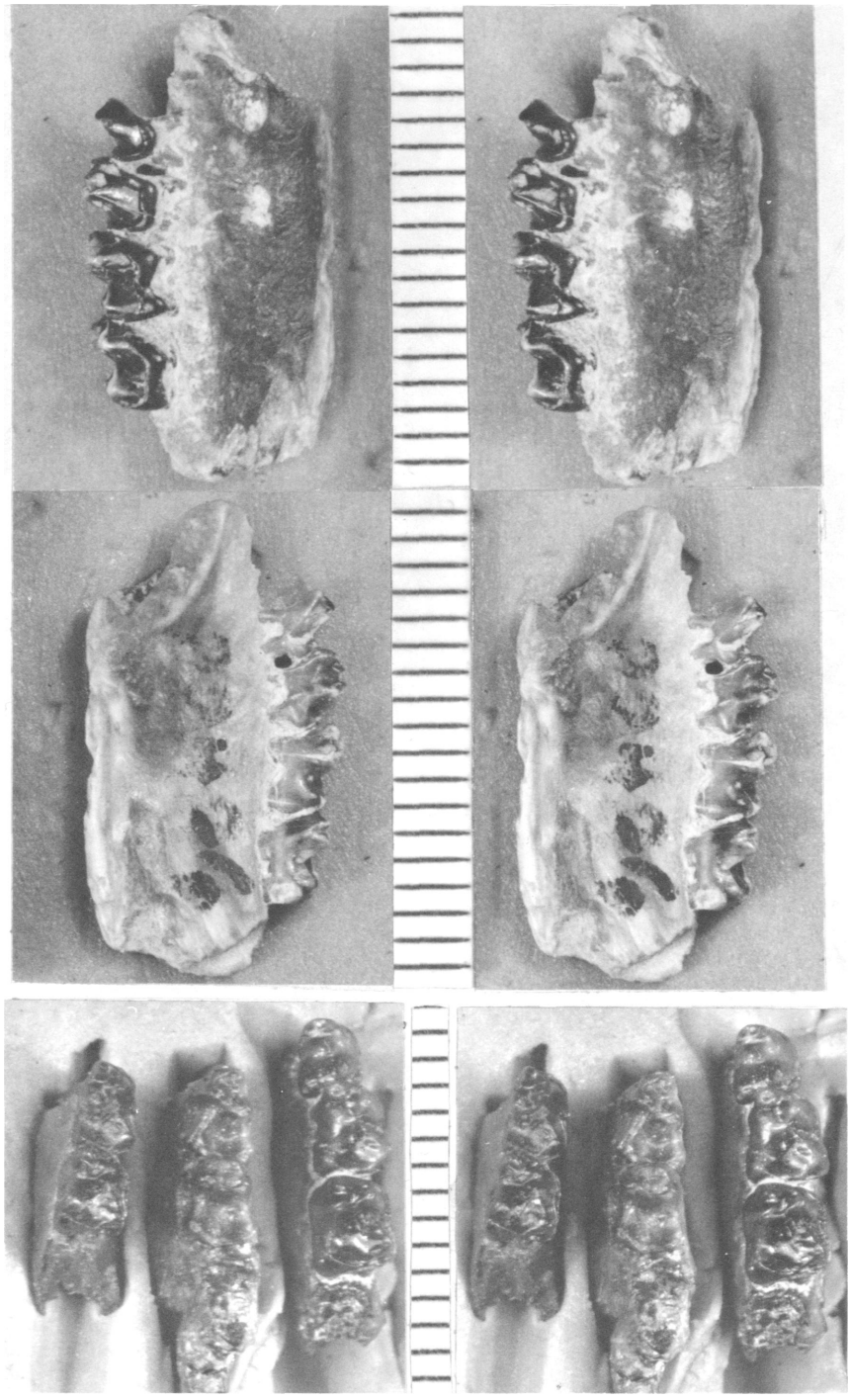


FIG. 31. Comparative lateral views of reconstructed left horizontal rami of *Anemorhysis tenuiculus* (below), *A. musculus* (middle), and *A. sublettensis* (above) to show the apparent loss of the second premolar through time. Arrows show canine (C) and second premolar (P_2). Scale represents 1 mm.

FIG. 32. *Anemorhysis tenuiculus*, USNM 22426, type of "*Tetonoides pearcei*," lower Wasatch beds, Washakie Basin, right P_3-M_2 (above and middle); AMNH 15066, Gray Bull beds, right P_4-M_2 (below right). *Anemorhysis* spp., AMNH 80956, East Alheit Pocket, Wasatch beds, right M_{1-2} (below left). *Anemorhysis* sp., CM 9426, type of "*Uintalacus nettingi*," lower fossiliferous zone Green River beds, left M_{1-3} (below center). Stereophotographs: above lateral, middle medial, and below occlusal views. Subdivisions on scale represent 0.5 mm.



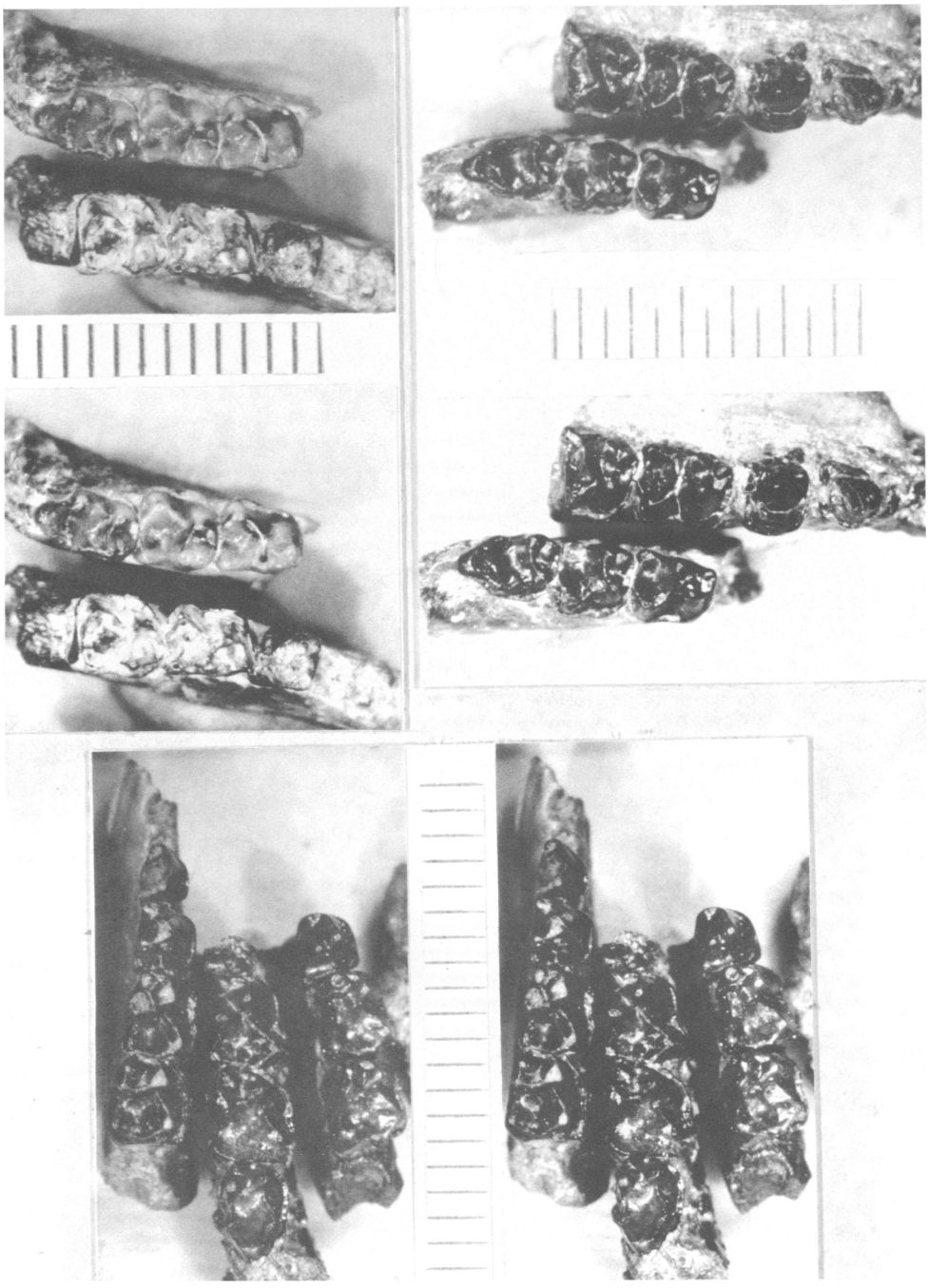


FIG. 33. *Anemorhysis tenuiculus*, USNM 22382, Wasatch beds, Washakie basin, left M_{1-3} (top above left); PU "69-19," Gray Bull beds, left P_4-M_2 (lower top left); PU 17683, Gray Bull beds, right P_3-M_2 (top above right); USNM 22799, Wasatch beds, upper Green River basin, right M_{1-3} (lower top right); USNM 22426, type of "*Tetonoides pearcei*," Wasatch beds, upper Green River basin, right P_3-M_2 (below left); PU 17326, Gray Bull beds, right M_{1-3} (below middle); and AMNH 15066, Gray Bull beds, right P_4-M_2 (below right). Stereophotographs: occlusal views, Subdivisions on scales represent 0.5 mm.

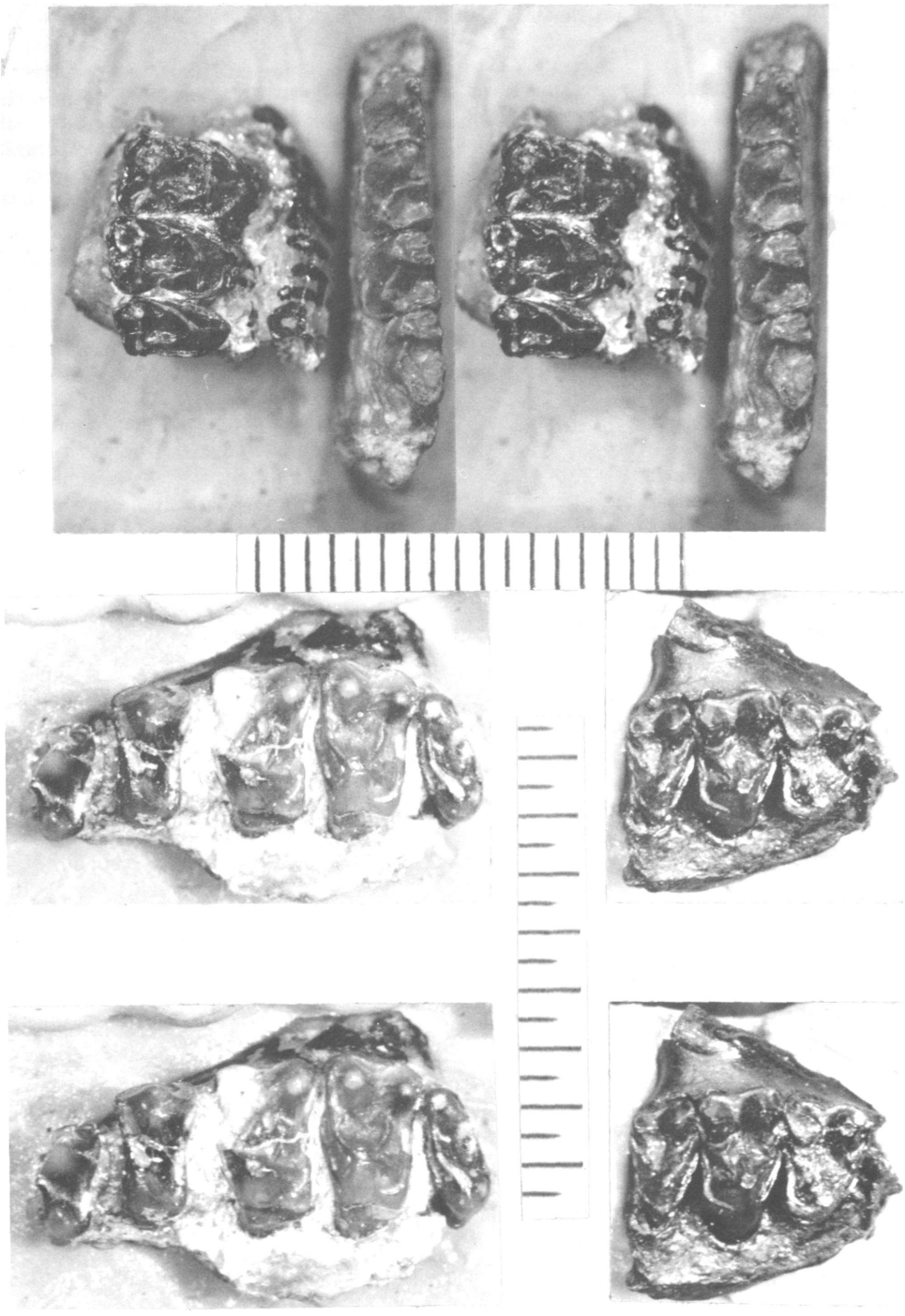


FIG. 34. *Anemorhysis tenuiculus*, PU 17357, right M^{1-3} (above left); PU 17232, left P_4-M_3 (above right); both Golden Valley beds. ?*Anemorhysis musculus*, YPM 18695, Yale loc. XLV, Lysite beds, left P^3-M^3 (below left); ?*Anemorhysis tenuiculus*, AMNH 59682, East Alheit Pocket, Wasatch beds, right M^{1-3} (above right). Stereophotographs: occlusal views. Subdivisions on scales represent 0.5 mm.

uncertain associations between upper and lower dentitions, and the consequently extremely confusing taxonomic picture, particularly in the publications spanning the time from 1950-1972 describing new taxa or attempting revision.

The following list represents those taxa that have been named (and a type specimen designated), the various concepts that have arisen from the new associations of various name bearing fossils (types), and indeterminate fossils, or names resulting from misspellings.

Tetonius musculus Matthew 1915, p. 463.
Tetonius tenuiculus Jepsen, 1930, p. 126.
Paratetonius ?sublettensis Gazin, 1952, p. 24.
Paratetonius ?tenuiculus: Gazin, 1952, p. 25.
Paratetonius musculus: Gazin 1952, p. 25.
Anemorhysis sublettensis: Gazin, 1958, p. 25.
Anemorhysis muscula: Gazin, 1958, p. 26.
Uintalacus nettingi Gazin, 1958, p. 29.
Tetonoides pearcei Gazin, 1962, p. 35.
"*Tetonius*" *tenuiculus*: Gazin, 1962, p. 35.
cf. *Anemorhysis minutus*: McKenna, 1960, p. 65.
Anemorhysis musculus: Guthrie, 1967, p. 17.

The earliest known species of the genus, *A. tenuiculus*, is known from early Wasatchian sediments (Gray Bull, Golden Valley, and Wasatch beds) of northeastern Wyoming, southwestern Wyoming, and North Dakota. *Anemorhysis musculus* is known from medial Wasatchian Lysite beds of the Wind River Basin, whereas *A. sublettensis* occurs in late Wasatchian upper Wasatch beds of western Wyoming (see especially Gazin 1952, 1958, 1962, and Jepsen, 1963, for correlation of *Anemorhysis* bearing strata and faunal information). What are the most reasonable systematic inferences that may be drawn from the samples allocated to this genus? To determine species boundaries is extremely difficult both because of the paucity of adequate samples and the geographical and stratigraphical spread of the known specimens. Because living species of strepsirhines, such as the various African galagines, are known to have distributions as extensive or greater than that of the entire *Anemorhysis* sample, distance is not considered as a meaningful aid to determine whether a sample for southwestern Wyoming should or should not be allocated to a species based on a northeastern sample.

Because none of the previous species is known to occur sympatrically, a relatively simple hypothesis might account for the seemingly bewildering chaos that taxonomists of this form have previously faced. If one considers this genus to be an evolving, single lineage then the significant morphological differences, such as the number and relative size of the antemolar dentition and the degree of molarization of the premolars, once put into a temporal frame, seem to make sense. It appears now that *A. tenuiculus* (incl. *A. pearcei*) is the oldest and most primitive, in having an unreduced P_2 and a semimolariform P_4. In *A. musculus*, the younger species from the Lysite, P_2 is extremely reduced, whereas in the youngest form, *A. sublettensis*, P_2 is completely lost and P_4 has become relatively less robust and what might be described as premolariform. It should be remembered that this is merely a model, but one which is not contradicted by the available evidence from the *Anemorhysis* samples. I have observed the extent and kind of molar variation displayed by *Anemorhysis*, the kind sometimes used as signifying specific or generic distinctions in the paleontological literature, in various samples of the same species of *Microcebus murinus* or *Galago crassicaudatus*, *Galago alleni* or in various samples of *Aotus trivirgatus*.

Table 6 presents the statistics for the combined samples of all three recognized species of *Anemorhysis*. It shows this genus to be extremely homogeneous. The high coefficient of variation of the L/PW ratio for P_4 (12.4), however, indicates that this aspect of the dental morphology might have been more variable in the genus, i.e., changed more extensively in the suggested lineage, than were other components, except relative dimensions of M^3.

The similarity of *Anemorhysis* to *Tetonius* is underlined by Gazin's (1958, p. 25) statement that, "The characters of the anaptomorphid *Anemorhysis* are essentially those earlier (Gazin, 1952) thought to characterize *Paratetonius* of Seton." The latter genus, however, was found to be based on a species synonymous with *Tetonius homunculus* (Gazin, 1958, p. 24).

Much of the discussion under the species below are closely pertinent to the generic evaluation.

Adaptations. Unlike in *Chlororhysis* or *Tetonius*, which have only a rudimentary meta-

conid on P_4, the earliest known *Anemorhysis*, *A. tenuiculus*, has a large metaconid on P_4 and thus also a protocristid running transversely on this tooth.

No single sample is large enough to meaningfully assess the upper and lower dentition of any of the species allocated to *Anemorhysis*. The Wasatchian Bitter Creek sample, recently collected by D. E. Savage, B. Waters, and H. Hutchison will undoubtedly go a long way to remedy this.

The heavy cingulids, the slightly molarized P_4, the gradually reduced antemolar dentition along with the increasing premolarization of the P_4 is

TABLE 6
Numerical Data for the Combined Samples of the Three Recognized Species of the Wasatchian *Anemorhysis*

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P^3								
L	1	1.35	–	–	–	–	–	–
W	1	1.92	–	–	–	–	–	–
P^4								
L	2	1.40-1.47	–	–	–	–	–	–
W	2	2.05-2.4	–	–	–	–	–	–
M^1								
L	3	1.65-1.80	–	1.750±0.050	0.087±0.035	5.361±2.189	–	–
AW	3	2.40-2.70	−0.359	2.583±0.093	0.161±0.066	6.740±2.752	–	–
L/AW	3	0.62-0.75	–	0.680±0.037	0.065±0.026	10.308±4.208	–	–
M^2								
L	3	1.61-1.74	–	1.657±0.042	0.072±0.030	4.731±1.931	–	–
AW	3	2.60-2.80	1.000	2.670±0.065	0.113±0.046	4.572±1.867	–	–
L/AW	3	0.62-0.62	–	0.620±0.001	0.001±0.000	0.195±0.080	–	–
M^3								
L	3	1.00-1.15	–	1.100±0.050	0.087±0.035	8.529±3.482	–	–
AW	3	1.91-2.20	−0.176	2.070±0.085	0.147±0.060	7.709±3.147	–	–
L/AW	3	0.48-0.60	–	0.534±0.037	0.064±0.026	12.923±5.276	–	–
P_4								
L	4	1.30-1.45	–	1.387±0.031	0.063±0.022	4.818±1.703	−1.129	2.227
PW	4	1.05-1.30	−0.476	1.192±0.052	0.104±0.037	9.299±3.288	−0.956	1.855
L/PW	4	1.00-1.33	–	1.172±0.068	0.137±0.048	12.375±4.375	−0.238	1.405
M_1								
L	12	1.65-2.00	–	1.772±0.034	0.117±0.024	6.714±1.371	0.737	−0.665
PW	12	1.27-1.71	0.685	1.482±0.038	0.133±0.027	9.169±1.872	−0.137	−0.552
AW	12	1.13-1.47	0.412	1.318±0.030	0.105±0.021	8.134±1.660	−0.517	−0.178
L/PW	12	1.08-1.33	–	1.200±0.023	0.079±0.016	6.703±1.368	−0.131	−0.678
M_2								
L	13	1.52-1.90	–	1.725±0.033	0.120±0.024	7.083±1.389	−0.004	−1.031
PW	13	1.35-1.80	0.802	1.550±0.036	0.128±0.025	8.438±1.655	0.197	−0.083
AW	13	1.33-1.70	0.828	1.531±0.033	0.119±0.023	7.932±1.556	−0.265	−0.604
L/PW	13	1.03-1.21	–	1.115±0.015	0.056±0.011	5.096±0.999	0.348	−0.401
M_3								
L	6	1.90-2.07	–	1.995±0.022	0.054±0.016	2.836±0.819	−0.814	2.847
PW	6	1.20-1.30	0.288	1.250±0.018	0.045±0.013	3.727±1.076	0.000	−1.875
L/PW	6	1.52-1.67	–	1.597±0.025	0.062±0.018	4.030±1.163	−0.001	−1.738

enigmatic. Judged from the alveoli, the central lower incisor was considerably enlarged. The molars are well suited for mesiolingual cutting, but this should be corroborated from the mandible and the temporomandibular joint, a task which must be delayed due to lack of appropriate specimens. The overall robust, beta thegosed molars (Every, 1972) might reflect a more phytophagous than zoophagous diet. On the other hand, if the enlarged incisors, once they become known, will show pointed, gracile cusps, features associated with prey catching, perhaps a primarily insectivorous way of life will then become a more suitable explanation for the total dental morphology of *Anemorhysis*.

Anemorhysis tenuiculus (Jepsen, 1930)
Figures 30-37; Tables 6-8

Tetonius tenuiculus Jepsen, 1930, p. 126.
Paratetonius ?tenuiculus: Gazin, 1952, p. 25.
Tetonoides pearcei Gazin, 1962, p. 35.
"Tetonius" tenuiculus: Gazin, 1962, p. 35.
Tetonoides tenuiculus: Gazin, 1962, p. 35.
Tetonoides cf. *T. pearcei*: Jepsen, 1963, p. 675.

Type. PU 13027, right P^3-M^3; collected from lower Gray Bull beds ±2 miles east of old Otto-Basin road crossing on Dorsey Creek, Big Horn Basin, Wyoming.

Hypodigm. The type, and USNM 22426 right mandible fragment (type of *A. pearcei*), and 22382 and 22383 from lower Wasatch beds, 1¼ miles south of Bitter Creek Station, Sweetwater County, Wyoming; USNM 22799, 1126 feet below the Tipton Tongue, on west side of Rock Springs uplift, Sweetwater County, Wyoming; PU 17231, 17232, 17336, 17357, from the Golden Valley Formation, Stark County, North Dakota; AMNH 15066 from lower Gray Bull beds, Willwood Formation, Big Horn Basin, Wyoming.

Geographical and Temporal Distribution.

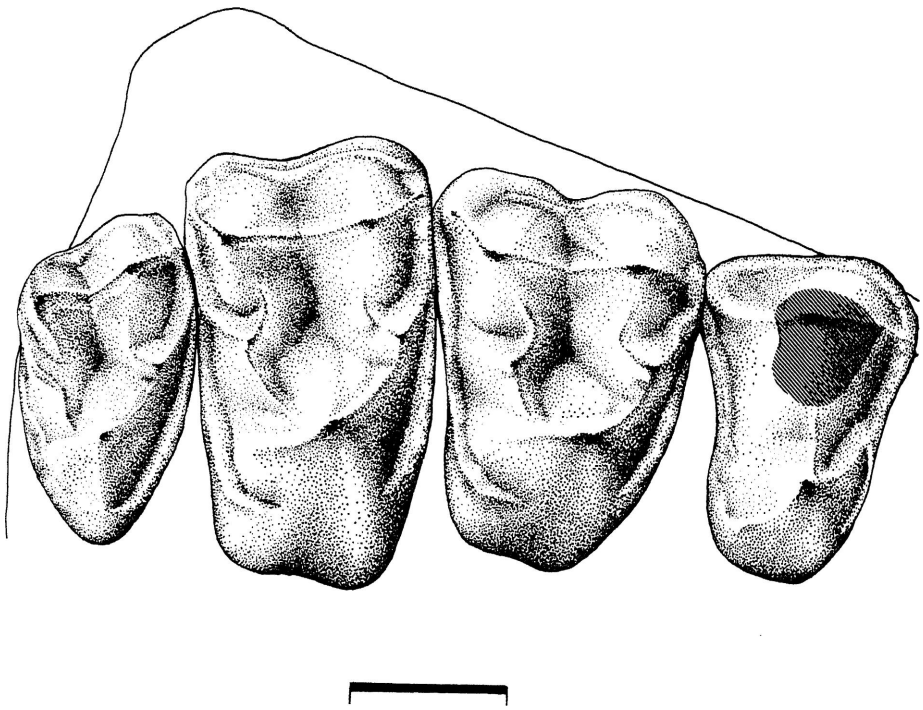


FIG. 35. *Anemorhysis tenuiculus*, PU 13027, type, lower Gray Bull beds, right P^3-M^3; occlusal view. Reconstruction shown by hatching. Scale represents 1 mm.

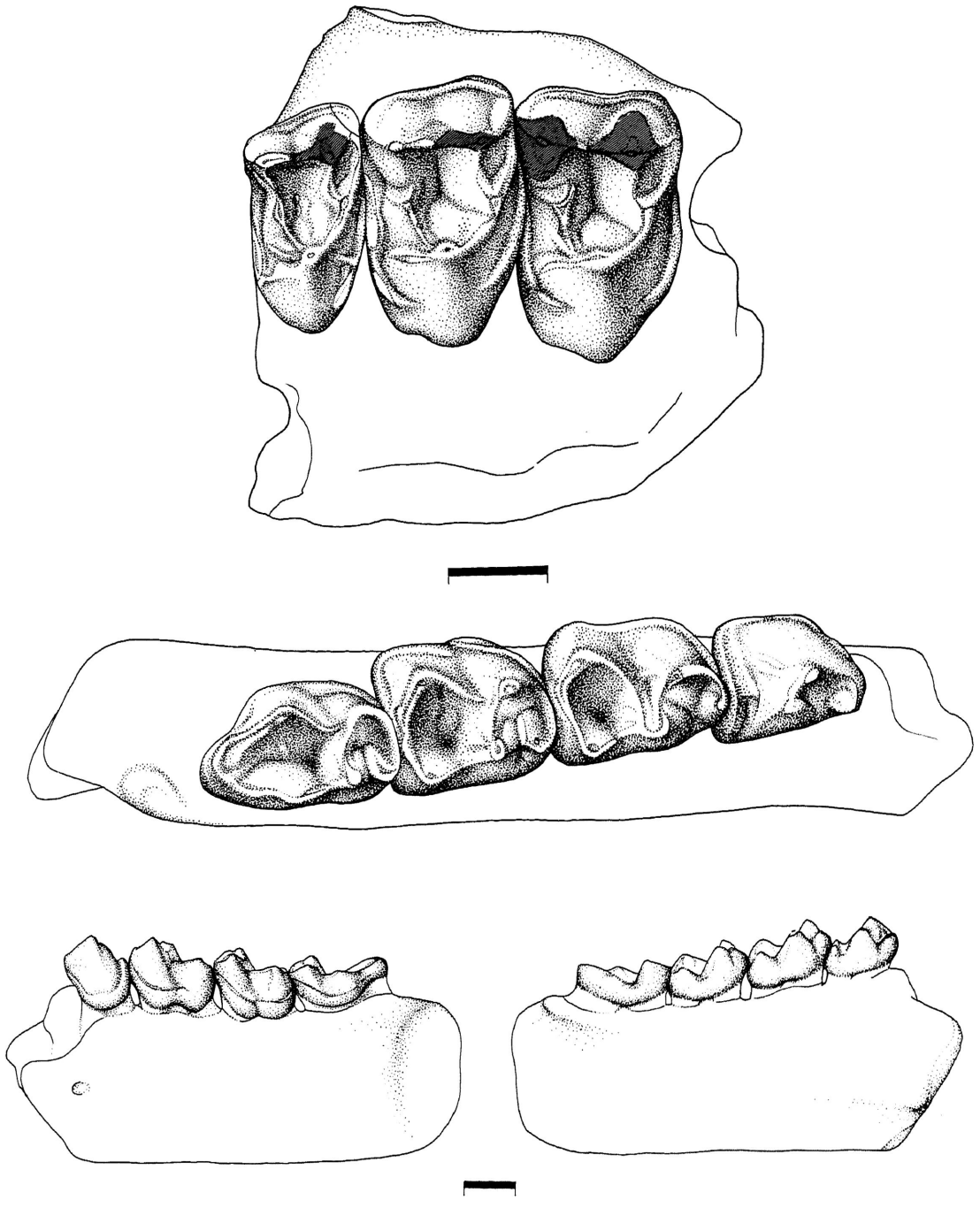


FIG. 36. *Anemorhysis tenuiculus*, PU 17357 (above), right M^{1-3}, occlusal view; PU 17232 (middle and below), left P_4-M_3, both Golden Valley beds; occlusal (middle), buccal (below left), and lingual (below right) views, respectively. Scales represent 1 mm.

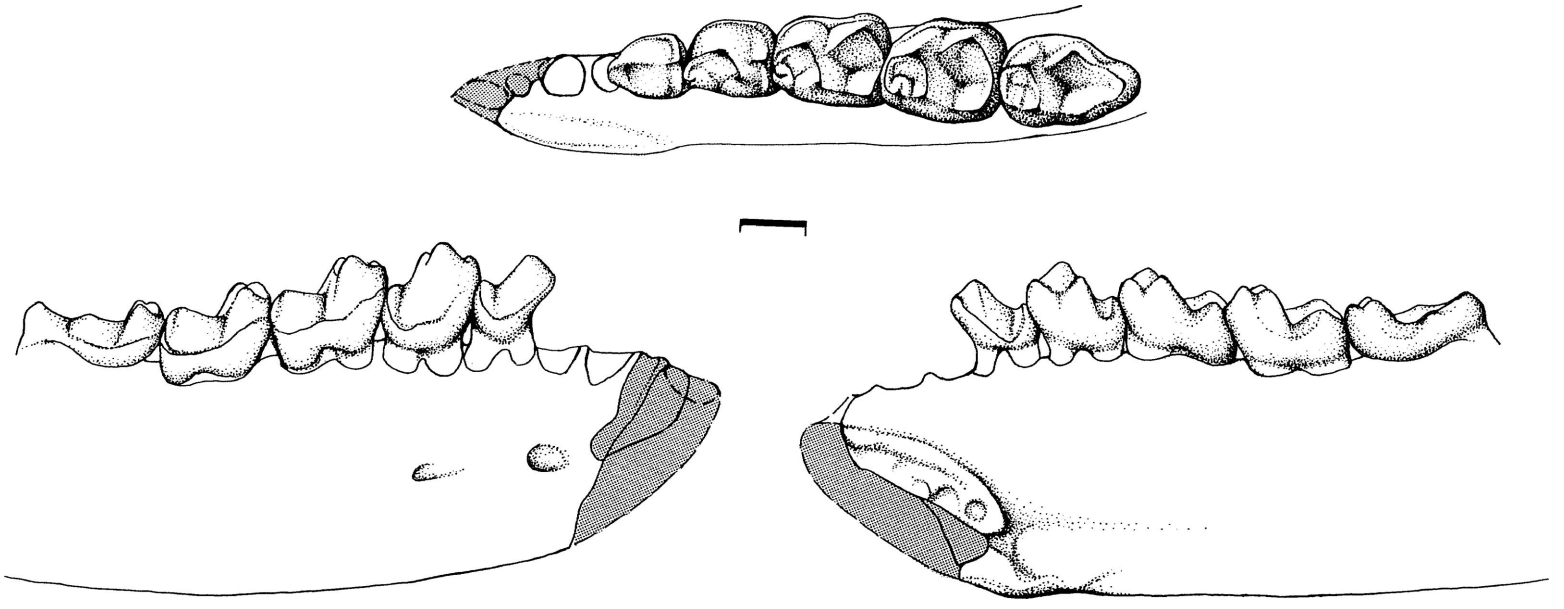


FIG. 37. *Anemorhysis tenuiculus*, right horizontal ramus with P_3-M_3, based on USNM 22382 and 22426, Wasatchian of Wyoming; occlusal (above), lateral (below left), and medial (below right) views. Reconstruction shown by stippling and broken lines. Scale represents 1 mm.

Early Wasatchian (earliest Eocene) of Wyoming, North Dakota, and Colorado.

Specific Diagnosis. Differences of *A. tenuiculus* from *A. sublettensis* and *A. musculus* appear to lie primarily in the proportions of the antemolar dentition. *Anemorhysis tenuiculus* has a relatively large P_2, whereas in the younger species, P_2 is rudimentary or absent.

Dental Formula. $I\frac{1,2}{1,2}; C\frac{1}{1}; P\frac{2,3,4}{2,3,4}; M\frac{1,2,3}{1,2,3}$.

Discussion. The holotype of *Anemorhysis tenuiculus* is a maxilla fragment, PU 13027, with P^4-M^3, whereas "*Tetonoides pearcei*" Gazin, 1962, was based on a mandible fragment, USNM 22426, containing P_3-M_2. These holotypes come from different geographical areas, from two different sedimentary basins, the Bighorn Basin and the Sand Wash Basin. There appears to be a rough faunal and presumably age equivalence between the lower Gray Bull and lower Wasatch

TABLE 7
Numerical Data for *Anemorhysis tenuiculus* from the Lower Gray Bull Beds and Golden Valley Beds

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P^4								
L	1	1.40	–	–	–	–	–	–
AW	1	2.05	–	–	–	–	–	–
L/AW	1	0.68	–	–	–	–	–	–
M^1								
L	2	1.65-1.80	–	–	–	–	–	–
AW	2	2.40-2.65	–	–	–	–	–	–
L/AW	2	0.62-0.75	–	–	–	–	–	–
M^2								
L	2	1.61-1.62	–	–	–	–	–	–
AW	2	2.60-2.61	–	–	–	–	–	–
L/AW	2	0.62-0.62	–	–	–	–	–	–
M^3								
L	2	1.15-1.15	–	–	–	–	–	–
AW	2	1.91-2.20	–	–	–	–	–	–
L/AW	2	0.52-0.62	–	–	–	–	–	–
P_4								
L	2	1.30-1.40	–	–	–	–	–	–
PW	2	1.20-1.30	–	–	–	–	–	–
L/PW	2	1.00-1.17	–	–	–	–	–	–
M_1								
L	6	1.70-2.00	–	1.850±0.045	0.110±0.032	6.168±1.781	−0.171	−0.781
PW	6	1.43-1.71	0.382	1.577±0.037	0.091±0.026	5.992±1.730	−0.313	1.816
AW	6	1.30-1.45	0.125	1.360±0.024	0.058±0.017	4.466±1.289	0.545	−0.552
L/PW	6	1.08-1.25	–	1.175±0.031	0.075±0.022	6.622±1.912	−0.680	−1.926
M_2								
L	8	1.65-1.90	–	1.775±0.034	0.096±0.024	5.599±1.400	0.0	−1.011
PW	8	1.45-1.80	0.732	1.600±0.041	0.116±0.029	7.509±1.877	0.452	−0.409
AW	8	1.50-1.70	0.856	1.590±0.030	0.086±0.021	5.558±1.389	0.267	−1.855
L/PW	8	1.03-1.21	–	1.112±0.019	0.055±0.014	5.105±1.276	0.223	0.354
M_3								
L	3	1.90-2.00	–	1.967±0.033	0.058±0.024	3.180±1.298	–	–
PW	3	1.25-1.30	0.500	1.267±0.017	0.029±0.012	2.469±1.008	–	–
L/PW	3	1.52-1.60	–	1.553±0.024	0.042±0.017	2.922±1.193	–	–

beds. There are, however, a few possibly important characters of the allocated local samples of the two areas which appear to contradict species synonymy. As the anterior dentition of *A. tenuiculus* becomes better known it is possible that a sufficient number of diagnostic characters may come to light to separate *A. pearcei* from *A. tenuiculus.* On the basis of the evidence available to me, however, I consider the southern sample ("*Tetonoides pearcei*") a representative of *A. tenuiculus.*

When Gazin (1962, pp. 34-36) described and characterized "*Tetonoides pearcei*" from early Wasatchian beds south of Bitter Creek Station, his specific diagnosis (p. 35) stated, "Size of teeth very close to those of "*Tetonius*" *tenuiculus* Jepsen, but paraconid and metaconid of M_2 and M_3 distinctly closer together, and anterior crest from protoconid on these teeth with greater anteroexternal deflection."

The generic diagnosis of "*Tetonoides*" given by him (pp. 34-35) was as follows: "Resembling *Tetonius* but P_4 relatively much smaller and lower crowned, with much better-developed paraconid and metaconid, better-defined talonid and well-defined external cingulum. Lower molars *Tetonius*-like but labial wall with a relatively much shorter slope and a well-developed cingulum. Apex of trigonid in lower molars transversely narrower and less compressed anteroposteriorly than in *Anemorhysis.*" Lower jaw specimens of "*Tetonius tenuiculus*" were described at that time. In 1915 Matthew (p. 463) allocated a lower jaw fragment, which was recovered from Gray Bull beds (AMNH 15066), to *T. musculus.* This specimen (fig. 32), now allocated to *A. tenuiculus*, does not show features in P_4 construction seen in *Tetonius.* Gazin (1962, p. 36), in fact, treated AMNH 15066 as a representative of *Tetonius* (i.e., *T. tenuiculus*) which should have either a) invalidated the allocation of Jepsen's species to *Tetonius*, or b) obliterated his generic distinction of both *Anemorhysis* and "*Tetonoides*" from *Tetonius.*

In the description of "*Tetonoides pearcei*" the most minute individual differences, without regard to variation in any of the known homogeneous anaptomorphine samples, were utilized as taxonomic criteria between *Anemorhysis sublettensis*, "*Anemorhysis muscula*" "*Tetonoides tenuiculus*," and "*Tetonoides pearcei.*" For example, Gazin (1962, p. 37) stated, "Were it not for the more noticeable upward convergence of the inner and outer walls of the lower molars, *T. pearcei* might well have been referred to *Anemorhysis. A. sublettensis*, a slightly smaller form, otherwise shows a shorter and broader trigonid and a relatively longer talonid. Anteroposterior development of the talonid also characterizes P_4 in *A. sublettensis.* M_3 in *Anemorhysis muscula* is very close in size to this tooth in *T. pearcei* (U.S.N.M. Nos. 22382 and 22799), and although M_3 is not known in *A. sublettensis*, the anteroposteriorly shorter trigonid and slightly more erect outer wall of the protoconid strongly suggest that *A. muscula* is more properly referred to *Anemorhysis* than to *Tetonoides.* I strongly suspect that *Tetonoides* is close to the line of development for *Anemorhysis.*"

Thus, although Gazin (1962) considered "*T. tenuiculus*" to be *Tetonoides*, he nevertheless described "*Tetonoides pearcei*" as the genero-type of *Tetonoides*, rather than make "*T. tenuiculus*" the type taxon.

Diagnosis of "*Tetonoides pearcei*" (i.e., *A. tenuiculus* as recognized here) was based on molar characters, which, in effect, do not differentiate this taxon from *A. musculus* and inadequately diagnose it in relation to *A. sublettensis.* Features of the antemolar dentition, however, clearly delineate this species from *A. sublettensis* and *A. musculus.* P_2, although single-rooted is well developed, whereas in *A. musculus* it was vestigial, and in *A. sublettensis*, according to Gazin's own (1952) account, it was absent.

A sample of small anaptomorphines from the Golden Valley Formation of Stark County, North Dakota, can be referred to *A. tenuiculus.* Jepsen (1963) has tentatively allocated that sample to *Tetonoides* cf. *T. pearcei.* On morphological and statistical evidence the allocation to *A. tenuiculus* appears certain. The P_4 morphology of the Golden Valley sample is virtually identical with that of USNM 22426 from the lower Wasatch or with that of AMNH 15066 from the lower Gray Bull beds.

One of the differences of questionable significance between the Golden Valley sample allocated to *A. tenuiculus* and the holotype of *A. tenuiculus* (PU 13027) lies in the construction of

the upper molars (PU 17357). In the holotype of *A. tenuiculus* from the Gray Bull M^1 is distinctly smaller than M^2, these conditions being essentially similar to those seen in *Tetonius homunculus*. In PU 17357 from the Golden Valley beds (figs. 34 and 36) M^1 is larger than M^2, and M^3, although smaller than M^2, is not a relatively very small tooth. I have found, however, size variation

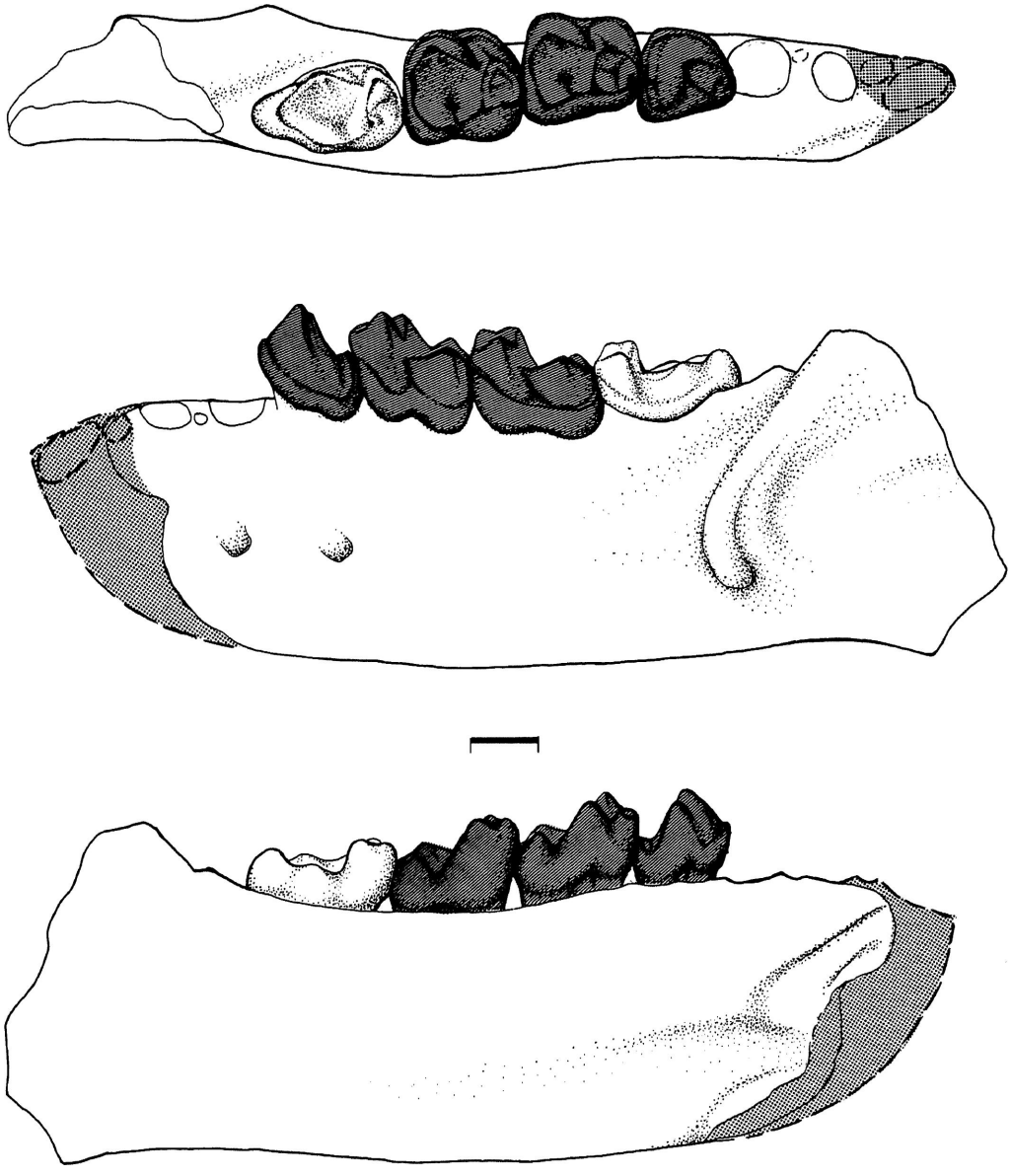


FIG. 38. *Anemorhysis musculus*, AMNH 12830, left horizontal ramus with M_3, remaining teeth shown are reconstructed, Wasatchian of Wyoming; occlusal (above), lateral (middle), and medial (below) views. Reconstruction shown by stippling, hatching, and broken lines. Scale represents 1 mm.

TABLE 8
Numerical Data for *Anemorhysis tenuiculus* from the Wasatch Beds

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P_3								
L	1	1.35	–	–	–	–	–	–
PW	1	1.01	–	–	–	–	–	–
L/PW	1	1.34	–	–	–	–	–	–
P_4								
L	1	1.45	–	–	–	–	–	–
PW	1	1.22	–	–	–	–	–	–
L/PW	1	1.19	–	–	–	–	–	–
M_1								
L	4	1.65-1.80	–	1.702±0.034	0.067±0.024	4.183±1.479	1.652	2.874
PW	4	1.40-1.52	0.260	1.445±0.027	0.054±0.019	4.005±1.416	1.188	0.605
AW	4	1.24-1.47	0.274	1.345±0.048	0.095±0.034	7.536±2.664	0.599	1.236
L/PW	4	1.11-1.24	–	1.179±0.027	0.054±0.019	4.845±1.713	−0.258	0.683
M_2								
L	3	1.60-1.84	–	1.687±0.077	0.133±0.054	8.553±3.492	–	–
PW	3	1.50-1.61	0.982	1.547±0.033	0.057±0.023	3.983±1.626	–	–
AW	3	1.40-1.55	0.564	1.500±0.050	0.087±0.035	6.255±2.553	–	–
L/PW	3	1.06-1.14	–	1.089±0.027	0.046±0.019	4.616±1.884	–	–
M_3								
L	2	2.00-2.07	–	–	–	–	–	–
PW	2	1.20-1.30	–	–	–	–	–	–
AW	2	1.30-1.47	–	–	–	–	–	–
L/PW	2	1.59-1.67	–	–	–	–	–	–

between adjacent teeth to be a very poor diagnostic feature. As I noted in the introductory part of the taxonomic section, in different specimens of *Microcebus murinus* from a single deme I have observed both $M^1>M^2>M^3$ and $M^1<M^2<M^3$ size relationships.

Judged from morphology and size, *A. tenuiculus* may also be represented in the East Alheit Pocket of the Four Mile assemblages. AMNH 59600, 59601, 69641, 59682, and 80956 may belong to this species.

Anemorhysis musculus (Matthew, 1915)
Figures 30, 31, 38, 39; Table 6

Tetonius musculus Matthew 1915, p. 463.
Paratetonius musculus (Matthew, 1915): Gazin, 1952, p. 25.
Anemorhysis muscula (Matthew, 1915): Gazin, 1958, p. 26.
Anemorhysis musculus (Matthew, 1915), Guthrie, 1967, p. 17.

Type. AMNH 12830, left mandible fragment with M_3 and alveoli of all other teeth; from the Lysite beds of the Wind River Formation, Cottonwood Draw, Fremont County, Wyoming.

Hypodigm. The type and possibly YPM 18695.

Geographical and Temporal Distribution. Medial Wasatchian (medial early Eocene) of Wyoming.

Specific Diagnosis. This species is intermediate between *A. tenuiculus* and *A. sublettensis* in having the P_2 in a vestigial form.

Dental Formula. $I\frac{1,2}{1,2}; C\frac{1}{1}; P\frac{2,3,4}{2,3,4}; M\frac{1,2,3}{1,2,3}$.

Discussion. Based on the proportions of the known alveoli of the antemolar teeth in the type of *A. musculus* and of *A. tenuiculus* (incl. *A. pearcei*), I conclude that these represent morphologically sufficiently distinct entities to be considered separate species. Comparisons of teeth other than M_3 are beset with the problem of lack of even referred teeth. Only M_3 is present in the

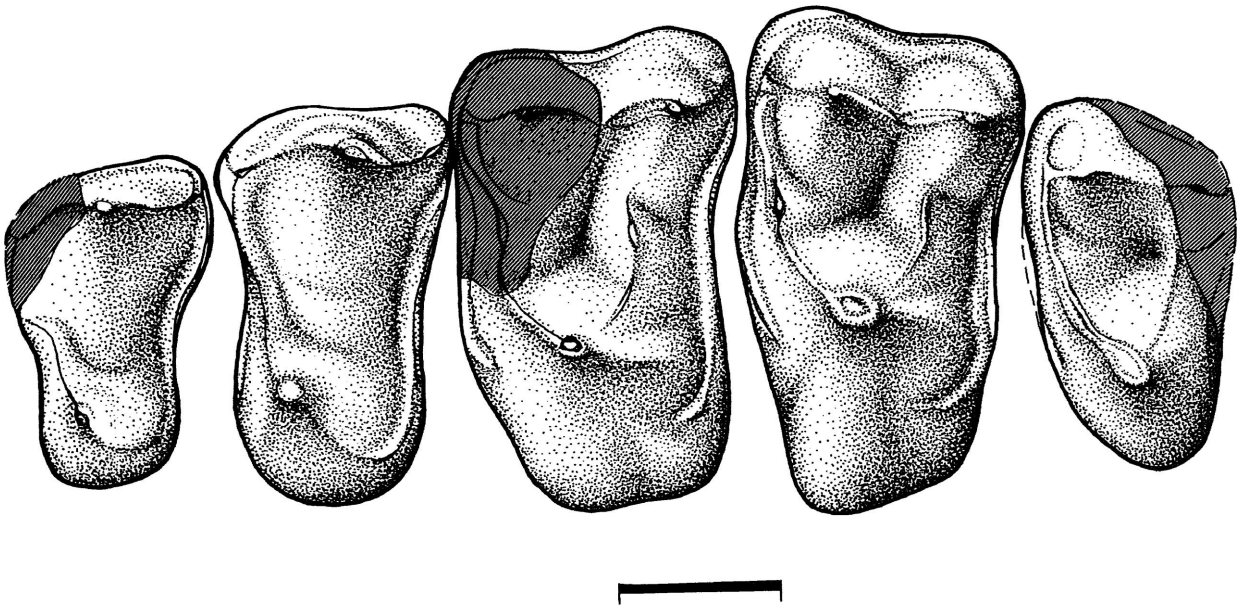


FIG. 39. ?*Anemorhysis musculus*, YPM 18695, Lysite beds, left P^3-M^3, occlusal view. Reconstruction shown by hatching and broken lines. Scale represents 1 mm.

Lysite holotype. AMNH 15066 from the lower Gray Bull beds, a right mandible fragment with P_4-M_2 (see fig. 32), shows exact proportions and size fit compared with the alveoli of the holotype. This specimen, as noted under *A. tenuiculus*, is of that species, the taxon probably ancestral to *A. musculus*.

Based on the morphology of P_4, *A. sublettensis* is distinct from *A. tenuiculus*, but because of lack of associated fourth premolars with the type of *A. musculus*, a similar distinction cannot be made. As I consider the molars relatively undiagnostic of the only specimen of *A. sublettensis* it is possible that the holotype of this species from the upper Wasatch beds is a specimen of the Lysite species *A. musculus*. Better samples both from the Gray Bull and upper Wasatch beds may provide evidence for or against this. From AMNH 12830, the holotype of *A. musculus*, it is clear that P_2 was vestigial, virtually all but lost, and other members of the Lysite deme might or might not have completely lacked this tooth. This is essentially the condition reported by Gazin (1952) for the type of *A. sublettensis*. Reduction of P_2 is such a common phyletic event among anaptomorphines, however, that this cannot be used as adequate evidence for species synonymy.

A partial left upper dentition, YPM 18695 (figs. 34 and 39) from Lysite equivalent beds, from the same horizon (traced along strike) as Yale loc. 45 (G. Mayer, personal commun.) appears to represent *Anemorhysis*. The teeth preserved are P^3-M^3 although the P^3, M^1, and M^3 are partly broken. I allocate it very tentatively as ?*A. musculus*. The upper dentition conforms in size to the type lower jaw. It differs significantly from the holotype of *A. tenuiculus*, PU 13027 (figs. 2, 5) from the lower Gray Bull beds. The major difference lies in YPM 18695 lacking a postmetaconule crista, thus having a single continuous crest on the distal half of the molars made up of the faint postprotocone crista and the premetaconule crista.

Anemorhysis sublettensis (Gazin, 1952)
Figures 30, 31, 40; Table 6

Paratetonius ?sublettensis Gazin, 1952, p. 24.
Anemorhysis sublettensis (Gazin, 1952), Gazin, 1958, p. 25.

Type. USNM 19205, left mandible fragment with P_4-M_2, from upper Wasatch beds, 12.2 miles north of Big Piney, Sublette County, Wyoming.

Hypodigm. The type only.

Geographical and Temporal Distribution. Late Wasatchian (late early Eocene) of Wyoming.

Specific Diagnosis. Differs from other species of *Anemorhysis* in having a relatively more slender P_4 and no P_2.

Dental Formula. Probably $I\frac{1,2}{1,2}$; $C\frac{1}{1}$; $P\frac{3,4}{3,4}$; $M\frac{1,2,3}{1,2,3}$.

Discussion. When the type specimen became available for restudy part of the mandible anterior to P_4 was missing. Gazin (1952, p. 25) related, however, that P_3 had two distinct roots. His description tells of an additional relatively large alveolus for a single-rooted tooth, a very small but deep alveolus, and a relatively large alveolus for the canine. Although Gazin (1952) suggested these alveoli were for P_2, P_1 (or the anterior root of P_2), and for the canine, they appear to be the same as in *A. musculus* in which these alveoli are for the canine and for the two incisors. P_2 is apparently lost; this condition is almost completely achieved by *A. musculus* in which P_2 is very small, squeezed lateral to P_3 and the canine.

As noted above, it is conceivable that *A. sublettensis* represents *A. musculus*.

The three known teeth of the holotype of this species are not an adequate basis for further discussion. Measurements of the holotype in millimeters are as follows: LP_4, 1.4; WP_4, 1.05; LM_1, 1.65; PWM_1, 1.27; AWM_1, 1.15; LM_2, 1.65; PWM_2, 1.36; AWM_2, 1.33.

Anemorhysis sp.
Figure 32

Anemorhysis "nettingi" Gazin, 1958 (=*Uintalacus nettingi* Gazin, 1958, p. 29).

This taxon, based on a single specimen, CM 9426, a left mandible fragment from the lower fossiliferous zone of the Green River Formation, Uinta Basin, Utah, now preserves only M_{1-2} and a badly damaged M_3. It once had a P_4 and the M_3 was undamaged. Notes by LeRoy Kay of the Carnegie Museum indicate that the damage occurred while casting (April, 1941) but, fortu-

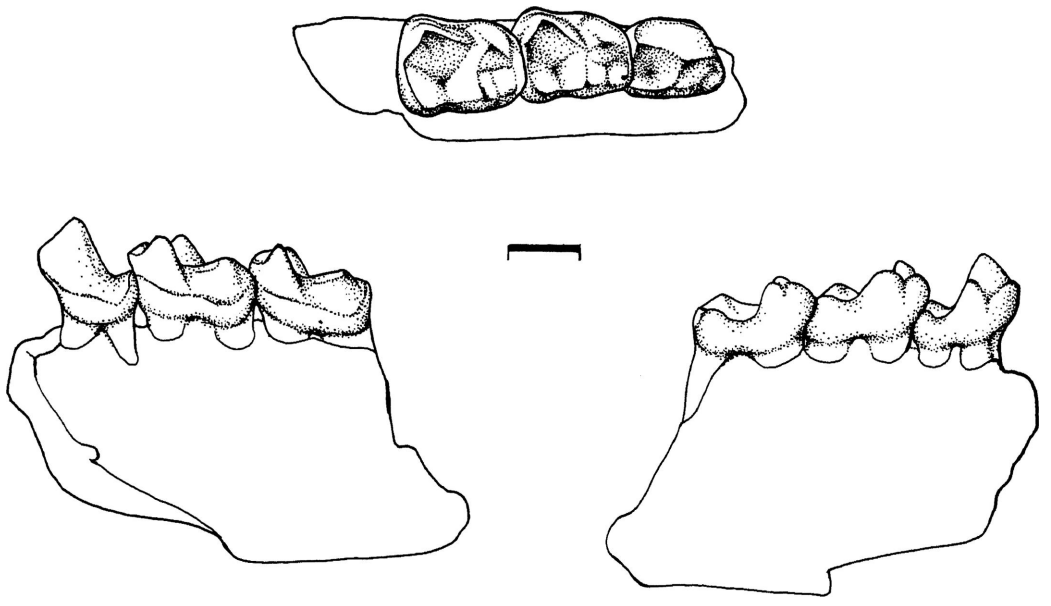


FIG. 40. *Anemorhysis sublettensis*, USNM 19205, type, Wasatch beds, upper Green River Basin, left mandible fragment with P_4-M_2; occlusal (above), buccal (below left), and lingual (below right) views. Scale represents 1 mm.

nately, casts of the type show the relatively well-preserved P_4 and M_3. Gazin's (1958, pl. 14, fig. 5) figure, probably based on the casts, shows P_4 without a metaconid. The cast, a poor one, nevertheless clearly shows that a metaconid, roughly equivalent in size to that of *Anemorhysis tenuiculus*, was broken off. M_3 shown by Gazin is also incorrectly restored. The generic characters given by Gazin (1958, p. 28) for "*Uintalacus*," based on Gazin's (1958) "*Uintalacus nettingi*," were as follows: "Lower molars resembling *Tetonius* but with less inflated basal portion, cusps more marginal in position with broader trigonid, somewhat as in *Anemorhysis*. P_4 unlike *Anemorhysis*, but resembles that in *Anaptomorphus* and *Tetonius*, although relatively smaller and less inflated appearing."

Gazin's generic diagnosis, based primarily on the configuration of a poor cast of P_4, is not adequate even on the species level. Although better material from the Green River Formation might prove this population distinct on the species level from either the Lysite or upper Wasatch *Anemorhysis*, this assumption is yet to be substantiated.

The figure of CM 9426 published by Gazin (1958, pl. 14, fig. 5) does not faithfully represent the specimen as now known.

ABSAROKIUS MATTHEW, 1915

Anaptomorphus: Loomis, 1906, p. 278.
Absarokius Matthew, 1915, p. 463.

Type Species. Absarokius abotti (Loomis, 1906).

Included Species. The type species, *A. noctivagus*, and *A. witteri*.

Geographical and Temporal Distribution. Medial Wasatchian to earliest Bridgerian (early Eocene to earliest medial Eocene) of Wyoming, and late Wasatchian of Colorado.

Generic Diagnosis. Anaptomorphines that differ from other genera of the subfamily chiefly in the enlargement of the third and fourth premolars. Although there is also a slight enlargement of P_4^4 in *Tetonius*, this condition is considerably surpassed in *Absarokius*. The central, enlarged lower incisors appear to be relatively smaller than those of *Tetonius*.

Discussion. Matthew (1915, p. 465) strongly

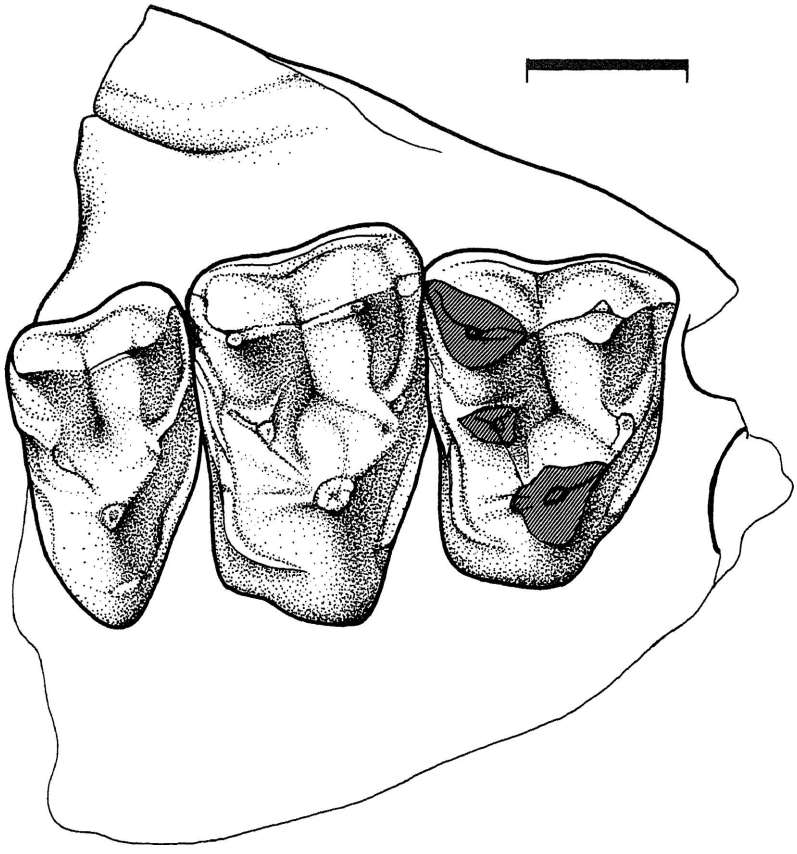


FIG. 41. ?*Anemorhysis tenuiculus*, AMNH 59682, East Alheit Pocket, right M^{1-3}; occlusal view. Reconstruction shown by hatching. Scale represents 1 mm.

suspected the close phyletic ties of *Absarokius* and *Tetonius* when he erected and defined the genus based on *A. abotti* and the then newly described *A. noctivagus*. He was held back, however, from deriving the *A. abotti-A. noctivagus* lineage directly from *Tetonius homunculus* by his interpretation of the dental formula of *T. homunculus* (see above). Kelly and Wood (1954, p. 344) and Morris (1954, p. 200) followed Matthew's interpretation of the dental formula of the latter but also the suggested close relationship of *Absarokius* to *Tetonius*.

The fact that *Tetonius homunculus* had two incisors, a canine, and three premolars in addition to the three molars renders the *Tetonius homunculus-A. abotti-A. noctivagus* lineage very probable. The moderately enlarged P_4 and the relatively large P_3 of *T. homunculus*, however, may be different enough from the species of *Absarokius* to maintain the generic distinction of *Absarokius* from *Tetonius*. The latter would have page priority were the differences found to be insufficient for generic separation in the future. The morphology of the molar teeth of *Absarokius* spp. is similar to those of *Tetonius homunculus*, the generic differences between the species being largely restricted to the third and fourth premolars.

The differences between the three known species of *Absarokius* are again restricted to the increase in the size of P_4 and the slight reduction of P_3 and the loss of P_2. There is, in addition, a

suggestion toward size increase and some minor morphological differences in the molars.

A striking feature of the symphyseal area of the preserved *Absarokius* mandibles, possibly a generic character, is the broad, wedge-shaped opening between the superior and inferior transverse tori of the symphysis.

The combined statistics of all the *Absarokius* samples (table 9) clearly show that the greatest evolutionary difference between the species of the genus lies in the size of P^3. This is possibly due to the inferred change in the relative size of P_3 in the *A. abotti-A. noctivagus* lineage. It is striking, however, how little size and proportion variation exists among the molars of the various samples of *Absarokius*. As shown by the morphology, selection affected the P_2^2-P_4^4 complex more than the molar dentition. The alveolar evidence indicates that the first incisor was reduced in *A. noctivagus* compared with that in *A. abotti*.

The view of Kelly and Wood (1954) that "...*Absarokius* represents a generically distinct line leading away from *Tetonius* . . . ," and that this distinction is shown by the anterior teeth, is questionable when one takes into consideration the evidence of P_4 from one of the most primitive known anaptomorphines, *Chlororhysis*. Although at present I am satisfied to maintain the taxonomic distinction on the genus level between *Tetonius* and *Absarokius*, the inference of these authors might not be valid when the adaptive differences are analyzed in detail. The morphological complex of characters of the teeth (and their functional correlates) had their beginning in *Tetonius homunculus*, particularly in the tall and bulky form of P_4. P_4 of *Tetonius homunculus* already indicates that for some reason a robust, tall, pointed premolariform tooth was favored by selection over the type of trenchant, relatively lower, and less bulky P_4 of *Chlororhysis*.

Adaptations. *Absarokius* is one of those unusual genera among omomyids which is known by three chronologically successive samples, two of which may be in an ancestor-descendant relationship to each other. In addition to this "near-phylogeny" the diagnostic characters are clearly derived compared with the tetoniinan morphotype. Thus, in a way, an ideal case for adaptational assessment is fulfilled. The mandible has become more robust, shorter, and the P_2 was lost from *A. abotti* to *A. noctivagus*. The third and fourth premolars have become progressively both transversely and mesiodistally more robust but have not become more molarized, the change being largely the result of the increased robustness of the paracones and protoconids. The first incisor is apparently somewhat more reduced in the more advanced *A. noctivagus*, and the symphysis is progressively more vertical in the younger species. Perhaps both the upper and lower dental arcades have become more U-shaped from *A. abotti* to *A. noctivagus*.

All these derived characters indicate a deemphasis of the anterior dentition and an emphasis shifted to the premolars. The robustness of the latter compels one to conclude that the forces incurred were considerable and resulted in a relative tooth size increase. This described shift may represent the change associated with specializations of a frugivore to certain hard fruits or nuts, and is not likely to be derived adaptations either for folivory or insectivory.

Absarokius abotti (Loomis, 1906)

Figures 42-49; Tables 9, 10, 12

Anaptomorphus abotti Loomis, 1906, p. 278.
Absarokius abotti (Loomis, 1906): Matthew, 1915, p. 463.

Type. AC 3479, right mandible fragment with P_3-M_3, Wind River Formation, Lysite beds, Wind River Basin, Wyoming.

Hypodigm. The type and AC 10156, 10201, 11009, 11192, AMNH 12756-12758, 14673, PU 13420, YPM 17465, 17471, 17473, 17476, 17478, 18639, 18684, 18685, 18690, 18691, 18693, 18699, 23176, 23196, all from the Lysite beds, Wind River Formation, Fremont County, Wyoming.

Geographical and Temporal Distribution. Medial Wasatchian (medial early Eocene) of Wyoming.

Specific Diagnosis. P_2 is present and jaw is slightly longer than in the younger *A. noctivagus*.

Dental Formula. $I\frac{1,2}{1,2}; C\frac{1}{1}; P\frac{2,3,4}{2,3,4}; M\frac{1,2,3}{1,2,3}$.

Discussion. The taxonomic status of this species is free of controversies, and referral of the

TABLE 9
Numerical Data for the Combined Samples of *Absarokius*

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P^3								
L	2	1.88-2.23	–	–	–	–	–	–
AW	2	2.13-2.45	–	–	–	–	–	–
L/AW	2	0.88-0.91	–	–	–	–	–	–
P^4								
L	7	2.15-2.45	–	2.271±0.036	0.095±0.025	4.337±1.159	0.967	1.795
AW	7	2.85-3.25	0.525	2.991±0.049	0.130±0.035	4.485±1.199	1.451	2.814
L/AW	7	0.71-0.81	–	0.760±0.011	0.030±0.008	4.101±1.096	−0.216	2.046
M^1								
L	9	1.97-2.25	–	2.120±0.033	0.099±0.023	4.805±1.133	−0.229	−1.209
AW	9	2.80-3.25	0.777	2.997±0.050	0.150±0.035	5.145±1.213	0.189	−0.751
L/AW	9	0.66-0.74	–	0.708±0.008	0.023±0.005	3.375±0.795	−1.228	3.071
M^2								
L	8	1.85-2.15	–	1.989±0.034	0.095±0.024	4.931±1.233	0.338	0.051
AW	8	3.05-3.50	0.686	3.255±0.048	0.137±0.034	4.334±1.084	0.473	0.538
L/AW	8	0.58-0.65	–	0.611±0.008	0.022±0.005	3.652±0.913	0.325	−0.993
M^3								
L	6	1.15-1.30	–	1.242±0.024	0.058±0.017	4.904±1.416	−0.668	−0.446
AW	6	1.95-2.15	−0.153	2.067±0.038	0.093±0.027	4.692±1.355	−0.165	−2.807
L/AW	6	0.53-0.65	–	0.602±0.017	0.042±0.012	7.246±2.092	−0.575	0.147
P_2								
L	2	0.90-1.45	–	–	–	–	–	–
PW	2	1.05-1.60	–	–	–	–	–	–
L/PW	2	0.86-0.91	–	–	–	–	–	–
P_3								
L	7	1.30-1.80	–	1.583±0.066	0.174±0.046	11.376±3.040	−0.532	−0.616
PW	7	1.28-2.00	−0.303	1.676±0.086	0.227±0.061	14.044±3.753	−0.637	1.012
L/PW	7	0.65-1.17	–	0.964±0.069	0.182±0.049	19.570±5.230	−0.718	0.035
P_4								
L	17	2.00-2.58	–	2.229±0.037	0.154±0.026	6.989±1.199	0.733	0.735
PW	17	1.90-2.75	0.859	2.170±0.051	0.209±0.036	9.770±1.675	1.344	2.705
L/PW	17	0.94-1.11	–	1.030±0.012	0.049±0.008	4.858±0.833	−0.322	−0.403
M_1								
L	19	2.20-2.60	–	2.284±0.026	0.114±0.019	5.071±0.823	1.588	2.236
PW	19	1.80-2.20	0.486	1.991±0.030	0.129±0.021	6.554±1.063	−0.036	−0.938
AW	19	1.60-2.05	0.255	1.814±0.026	0.111±0.018	6.227±1.010	−0.093	0.232
L/PW	19	1.04-1.28	–	1.150±0.016	0.069±0.011	6.067±0.984	0.104	−0.750
M_2								
L	23	2.03-2.63	–	2.216±0.029	0.140±0.021	6.401±0.944	1.666	3.436
PW	23	1.75-2.25	0.514	1.993±0.029	0.137±0.020	6.969±1.028	0.290	−0.567
AW	23	1.65-2.28	0.471	1.984±0.033	0.159±0.023	8.106±1.195	0.033	−0.305
L/PW	23	1.00-1.26	–	1.115±0.015	0.074±0.011	6.725±0.992	0.161	−0.774
M_3								
L	15	2.10-3.10	–	2.407±0.079	0.306±0.056	12.946±2.364	0.933	0.034
PW	15	1.25-1.90	0.843	1.531±0.051	0.196±0.036	13.038±2.380	0.368	−0.415
AW	15	1.40-2.03	0.769	1.668±0.048	0.185±0.034	11.258±2.055	0.703	−0.349
L/PW	15	1.40-1.80	–	1.577±0.031	0.119±0.022	7.674±1.401	0.603	−0.057

TABLE 10
Numerical Data for Specimens of *Absarokius abotti* from Lysite Beds, Wind River Formation, Wind River Basin, Wyoming

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P^3								
L	1	2.23	–	–	–	–	–	–
AW	1	2.45	–	–	–	–	–	–
L/AW	1	0.91	–	–	–	–	–	–
P^4								
L	4	2.20-2.30	–	2.250±0.020	0.041±0.014	1.928±0.682	0.000	1.500
AW	4	2.90-3.25	0.899	3.020±0.079	0.159±0.056	5.592±1.977	1.610	2.538
L/AW	4	0.71-0.77	–	0.746±0.013	0.027±0.009	3.789±1.340	−1.557	2.606
M^1								
L	5	1.97-2.23	–	2.100±0.044	0.098±0.031	4.924±1.557	0.000	−0.245
AW	5	2.83-3.13	0.528	2.972±0.058	0.129±0.041	4.568±1.445	−0.046	−2.237
L/AW	5	0.66-0.74	–	0.707±0.014	0.031±0.010	4.665±1.475	−1.121	2.240
M^2								
L	5	1.90-2.00	–	1.966±0.019	0.042±0.013	2.253±0.713	−1.166	0.581
AW	5	3.18-3.35	−0.252	3.232±0.032	0.072±0.023	2.336±0.739	1.496	1.805
L/AW	5	0.58-0.63	–	0.609±0.009	0.021±0.007	3.609±1.141	−0.229	−2.230
M^3								
L	4	1.15-1.30	–	1.225±0.032	0.065±0.023	5.599±1.979	0.000	−1.200
AW	4	2.00-2.15	−0.447	2.075±0.043	0.087±0.031	4.434±1.568	0.000	−6.000
L/AW	4	0.53-0.65	–	0.592±0.024	0.048±0.017	8.552±3.024	0.104	0.763
P_2								
L	1	0.90	–	–	–	–	–	–
PW	1	1.05	–	–	–	–	–	–
L/PW	1	0.86	–	–	–	–	–	–
P_3								
L	2	1.70-1.80	–	–	–	–	–	–
PW	2	1.50-1.70	–	–	–	–	–	–
L/PW	2	1.06-1.13	–	–	–	–	–	–
P_4								
L	10	2.00-2.25	–	2.144±0.028	0.089±0.020	4.271±0.955	−0.664	−0.471
PW	10	1.90-2.28	0.696	2.064±0.037	0.118±0.026	5.882±1.315	0.166	−0.178
L/PW	10	0.96-1.11	–	1.040±0.013	0.042±0.009	4.134±0.924	−0.644	0.788
M_1								
L	13	2.20-2.50	–	2.254±0.025	0.090±0.018	4.072±0.799	1.990	4.110
PW	13	1.80-2.12	0.406	1.970±0.035	0.125±0.025	6.493±1.273	−0.278	−1.515
AW	13	1.60-1.95	0.172	1.789±0.031	0.110±0.022	6.277±1.231	−0.359	−0.774
L/PW	13	1.04-1.28	–	1.147±0.019	0.070±0.014	6.196±1.215	0.246	−0.615
M_2								
L	14	2.03-2.33	–	2.196±0.023	0.085±0.016	3.941±0.745	−0.673	0.263
PW	14	1.80-2.18	0.201	1.980±0.030	0.113±0.021	5.809±1.098	0.257	−0.574
AW	14	1.75-2.20	0.049	1.981±0.035	0.131±0.025	6.747±1.275	−0.114	−0.772
L/PW	14	1.00-1.26	–	1.112±0.019	0.071±0.013	6.503±1.229	0.630	0.011
M_3								
L	8	2.10-2.40	–	2.211±0.035	0.099±0.025	4.640±1.160	0.774	0.587
PW	8	1.25-1.58	0.550	1.410±0.046	0.130±0.032	9.472±2.368	−0.194	−1.818
AW	8	1.40-1.75	0.299	1.567±0.040	0.114±0.029	7.516±1.879	0.386	−0.365
L/PW	8	1.42-1.80	–	1.577±0.044	0.125±0.031	8.147±2.037	0.678	−0.185

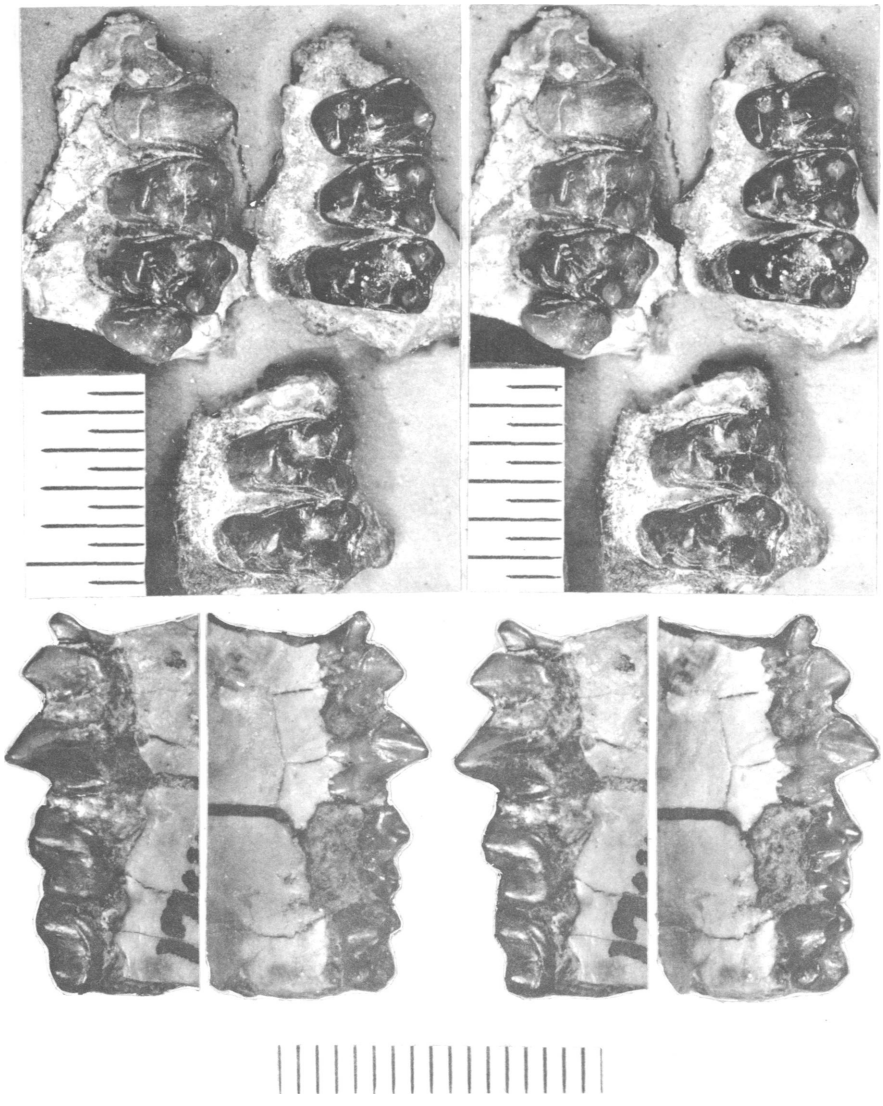


FIG. 42. *Absarokius abotti*, YPM 18699, left P^4-M^3 (above left); YPM 17483, left P^4-M^2 (above right); YPM 18684, left M^1-M^2 (middle); and YPM 17476, right P_2-M_2 (below), all from Lysite beds. Stereophotographs: above and middle occlusal, below left lateral, and below right medial views. Subdivisions on scales represent 0.5 mm.

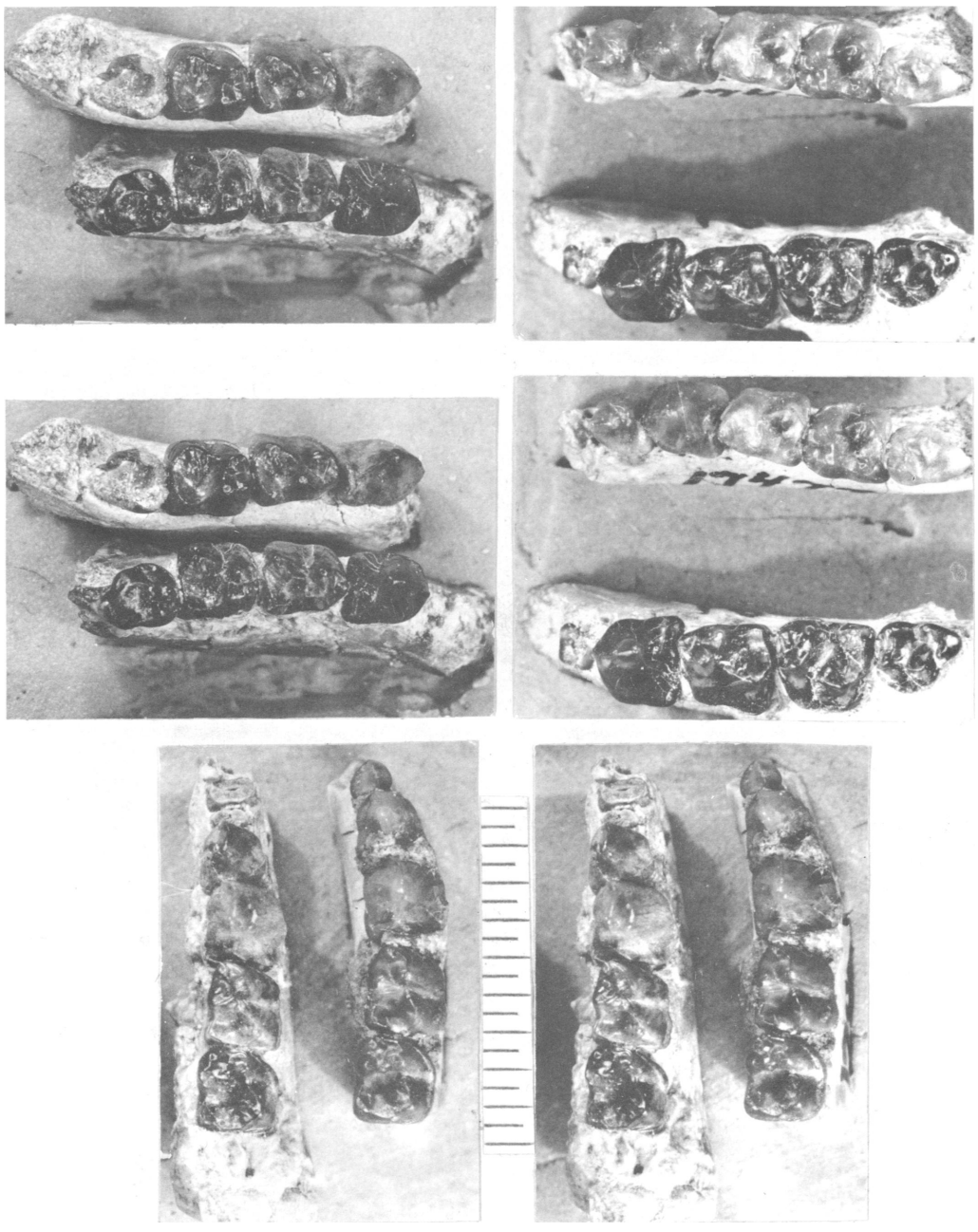


FIG. 43. *Absarokius abotti*, YPM 23176, left P_4-M_3 (above left top); YPM 23196, left P_4-M_3 (above left bottom); YPM 17473, right P_3-M_3 (above right top); YPM 18691, left P_4-M_3 (above right bottom); YPM 17478, right P_3-M_2 (below left); and YPM 17476, right P_2-M_2 (below right); all from Lysite beds. Stereophotographs: occlusal views. Subdivisions on scale represent 0.5 mm.

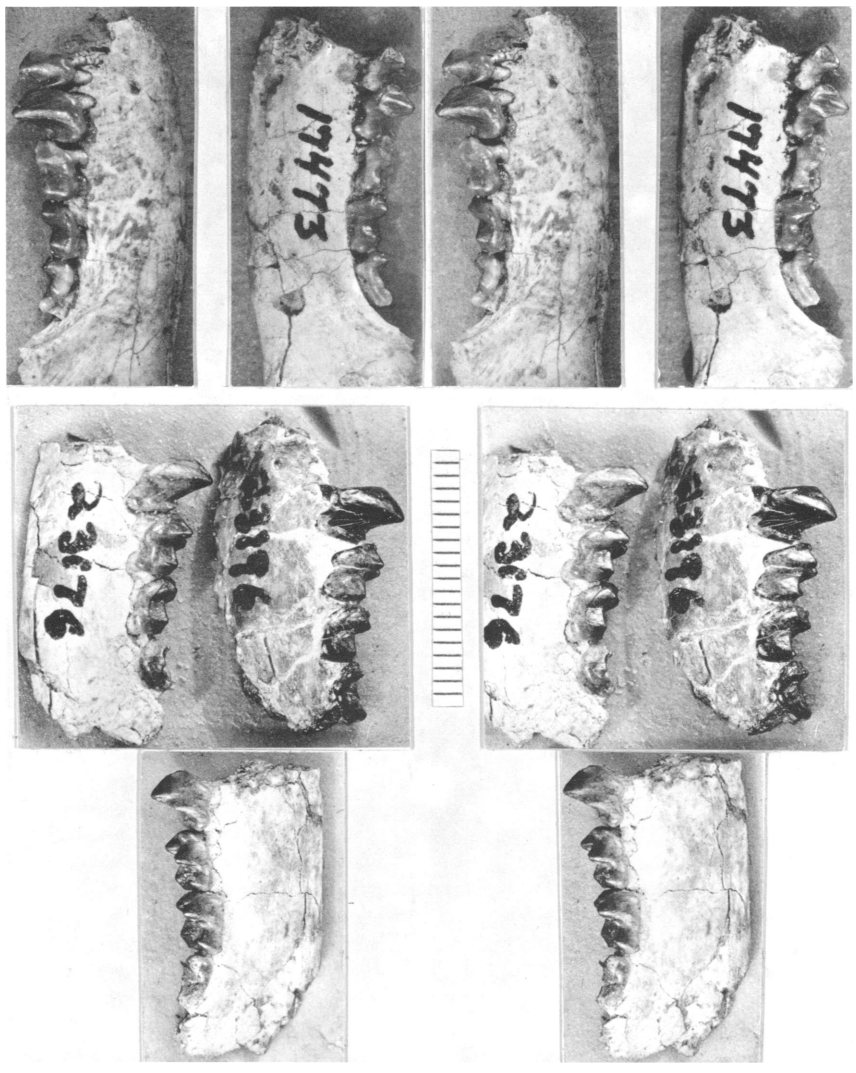


FIG. 44. *Absarokius abotti*, YPM 17473, right P_3-M_3 (above); YPM 23196, left P_4-M_3 (middle right); YPM 23176, left P_4-M_3 (middle left and below), all from Lysite beds. Stereophotographs: above left and middle lateral, and above right and below medial views. Subdivisions on scale represent 0.5 mm.

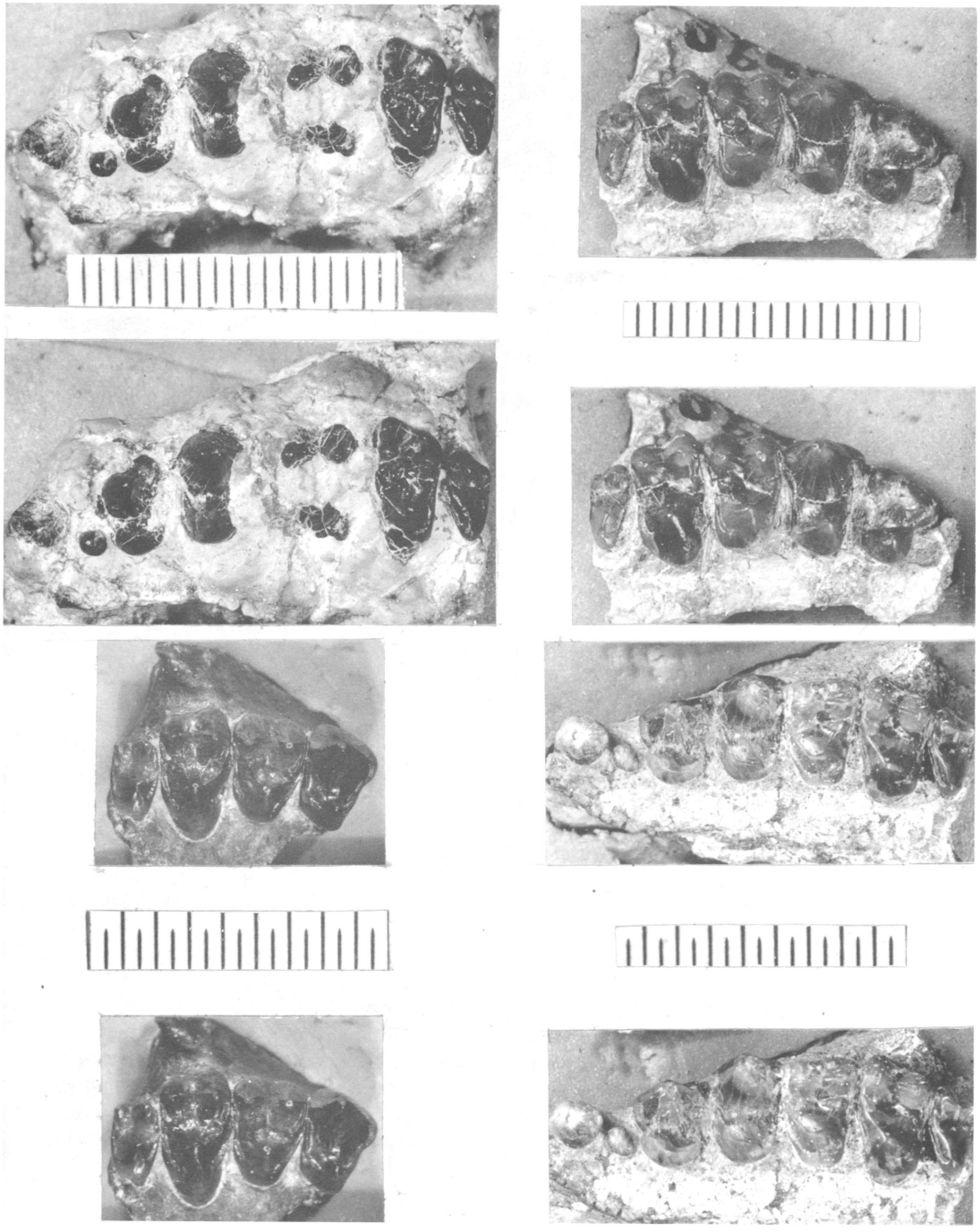


FIG. 45. *Absarokius abotti*, YPM 23177, left C-M^3 (above left); YPM 18690, right P^3-M^3 (above right); YPM 18686, left C-M^3 (below right), all from Lysite beds. *Absarokius noctivagus*, AMNH 14663, Lost Cabin beds, left P^4-M^3 (below, left). Stereophotographs: occlusal views. Subdivisions on scales represent 0.5 mm.

specimens followed past practices, namely that *Absarokius* from the Lysite beds of the Wind River Formation belong to this species. Kelly and Wood (1954, p. 343) discussed variation in the cheek tooth morphology, and Guthrie (1967, p. 17) recently published statistics on this species, using a larger sample for most of the lower teeth. My statistics differ slightly because I use slightly different parameters (my anterior and posterior width of the lower teeth vs. Guthrie's width, or my width of the upper teeth vs. his, for example). Because I measured the specimens treated in this monograph by the same methods and at the same points, I publish my own data as a supplement to Guthrie's valuable statistics.

UW 1644, from approximately the Gray Bull level (*fide* P. O. McGrew, personal commun.) of the Red Desert area, as reported by Gazin (1962, p. 37), is an unusually small *Absarokius*. The three molars of this specimen are very small (see fig. 48), and the dimensions of P_4 are matched only by two P_4s of *A. abotti*, those of YPM 18685 and 17476, both from the Lysite equivalent beds of the "Buffalo Basin" in the Big Horn Basin.

Because the molars of UW 1644 are much smaller than any other known *Absarokius* they have not been included in the statistics of *A. abotti*. Although on the basis of morphology I would allocate the Wyoming specimen to *A. abotti*, its unusually smaller molar dimensions may indicate its provenance from a hitherto unknown small population of the genus. UW 1644 and YPM 17476, 27791, and 28205 are specimens known to me which clearly preserve an alveolus for P_2 or actually have this tooth. There are indications of a P_2 alveolus also on the somewhat poorly preserved AMNH 14673. Whenever the anterior part of the maxilla is known, an alveolus or the actual P^2 is present (figs. 45-46). There is no doubt that *A. abotti* had a persistent upper and lower second premolar. Although the canine is reported by Bown and Gingerich (1972), there are no specimens of the incisors known for this species.

As Matthew (1915) and Kelly and Wood (1954) suggested, *A. abotti* of the Lysite beds appears to have evolved into *A. noctivagus* of the younger Lost Cabin and Huerfano sediments, primarily in increasing the relative size of fourth premolars and by eliminating the second premolars. There does not seem to be a major phyletic trend toward a larger size, although small overall average size increase is indicated by the statistics. In *A. abotti* the cingula on the molars are stronger than those of *A. noctivagus*, although this occurs more often in the younger species as a broad buccal fold on both the upper and lower molars.

Absarokius noctivagus Matthew, 1915

Figures 45, 48-54; Tables 1, 11, 12

Absarokius noctivagus Matthew, 1915, p. 465.

Type. AMNH 15601, right mandible fragment with P_3-M_3, Wind River Formation, Lost Cabin beds, Wind River Basin, 5 miles north of Parker Spring.

Hypodigm. The type, and AMNH 14663, 15602, USNM 18439, YPM 17488, from Lost Cabin beds, Wind River Formation, Wind River Basin; USNM 19198 and 22264, North of Big Piney, Wyoming (for locality data see Gazin, 1958, 1962); AMNH 55152, 55154, 55155, 55215, 55217, 55218, 55270, 55292, Huerfano Formation, Colorado (for locality data see Robinson, 1966).

Geographical and Temporal Distribution. Late Wasatchian (late early Eocene) of Wyoming and Colorado.

Specific Diagnosis. P_2 is lost and the jaw slightly shortened and more robust compared with the older *A. abotti*.

Dental Formula. $I\frac{1,2}{1,2}$; $C\frac{1}{1}$; $P\frac{2,3,4}{3,4}$; $M\frac{1,2,3}{1,2,3}$.

Discussion. The number of specimens available for *A. noctivagus* is not so extensive as that for *A. abotti*, yet an adequate characterization of most of the dentition is possible (figs. 52-53).

Robinson (1966, p. 33) named a new subspecies *A. noctivagus nocerai*, basing the name on AMNH 55215 (fig. 51) from loc. II of the upper faunal zone of the Huerfano Formation. This specimen is virtually identical with the type of *A. noctivagus* from the Lost Cabin beds. Although some Huerfano specimens have a larger PW/L ratio (AMNH 55218, loc. I) of the first and second molars and of the third molars (AMNH 55152, 55217, loc. III) than those of Lost Cabin *Absarokius*, and there is an average size difference between M_2 of the Huerfano and Lost Cabin samples as noted by Robinson (1966, p.

33), I see no justification for a subspecies taxonomy in *Absarokius noctivagus*. The Huerfano *Absarokius* of localities I, II, and III is morphologically inseparable from *A. noctivagus* and the size differences do not, in my opinion, warrant criteria for formal discrimination. Even if a case may be made for the subspecies distinction of the Huerfano sample, this practice would precipitate a surge in subspecies nomina among the primarily dentally known Eocene primates. This, I believe, would give rise to an even greater degree of confusion than that which has existed on the species level.

The differences between the molars of *A. noctivagus* and those of its probable direct ancestor *A. abotti* are very difficult to sort out. They mostly involve the changes in the structure of the third and fourth premolars as pointed out above. Individual specimens with the molars or only the upper molars with a P^4 are very difficult to allocate (compare, for example, PU 13420 and AMNH 55154, fig. 49). Although these two specimens come from different localities (red badlands west of Cottonwood Creek, north of Lost Cabin vs. Huerfano loc. III) and are of different age, they look virtually alike. Yet PU 13420 is probably *A. abotti* and AMNH 55154 is *A. noctivagus* (see P^3-M^1 from Huerfano loc. III, AMNH 55155, fig. 49).

In *A. noctivagus* the buccal border of P_4 bulges and folds down ventrally on the alveolar border of the mandible to a greater degree than this is seen in *A. abotti*. The protoconid of P_4 appears to rise relatively higher in the former than in the Lysite species.

As P_2 becomes lost and P^2 extremely reduced due to shortening of the snout and mandible, the morphology of P_3 is altered probably as a result of onotogenetic tooth crowding at first. The mesial margin of P_3 is folded so the talonid of the canine can fit into this space. The corresponding changes of P^3 involve a slightly greater lingual rotation than in *A. abotti*.

Absarokius witteri Morris, 1954
Figures 55, 56; Table 9

Absarokius witteri Morris, 1954, p. 200.

Type. PU 14972, left mandible fragment with P_3-P_4, M_2-M_3 and alveoli for the two incisors, C, and M_1, from Cathedral Bluffs Tongue, Wasatch Formation, Washakie Basin, sect. 33, T. 19 N, R. 95 W, Sweetwater County, Wyoming.

Hypodigm. The type only.

Geographical and Temporal Distribution. Early Bridgerian (earliest medial Eocene) of Wyoming.

Specific Diagnosis. Absarokius witteri is slightly larger than either *A. abotti* or *A. noctivagus*. Unlike the Wasatchian species, *A. witteri* has a rather robust P_4 on which the paracristid, a trenchant crest in the former species, is rounded off. Unlike the other known *Absarokius*, *A. witteri*, appears to have distinctly crenulated molar talonids.

Dental Formula. $I\frac{1,2}{1,2}$; $C\frac{1}{1}$; $P^{?},\frac{3,4}{3,4}$; $M\frac{1,2,3}{1,2,3}$.

Discussion. This species is known by a single specimen which renders some of the comparisons with the more abundant samples of *Absarokius* tenuous. As noted in the original description, and as it can be appreciated from figures 55 and 56, the type of *A. witteri* is larger than other known specimens of *Absarokius* and, therefore, it is assumed that the large size was representative of *A. witteri* populations in general. The slight phyletic trend of size increase exhibited by the Wasatchian *Absarokius* populations was apparently carried farther in the earliest Bridgerian *Absarokius*.

Wrinkling of the enamel on the molar crowns of the type of *A. witteri* is rare among known specimens of the genus, although the molars of the type of *A. noctivagus* are also fairly crenulated.

Judged from the proportions of the mandible anterior to P_3, additional reduction of the anterior dentition occurred from a probable *A. noctivagus* ancestral population, resulting in the size reduction of the canine and the incisors.

(Morris (1954, p. 200) judged the protoconid of P_4 to be bunodont. Because there is fairly heavy wear on the protocristid and paracristid as well as on the protoconid (some flaking of the enamel is also involved) I cannot determine the degree to which the protoconid might be rounded off or blunter than that in stratigraphically older populations of the genus. P_3 is, however, less damaged and worn than P_4, and on this tooth the protoconid does not look especially bunodont. Although the P_4 is a very large, wide tooth, the kind one might assume capable of

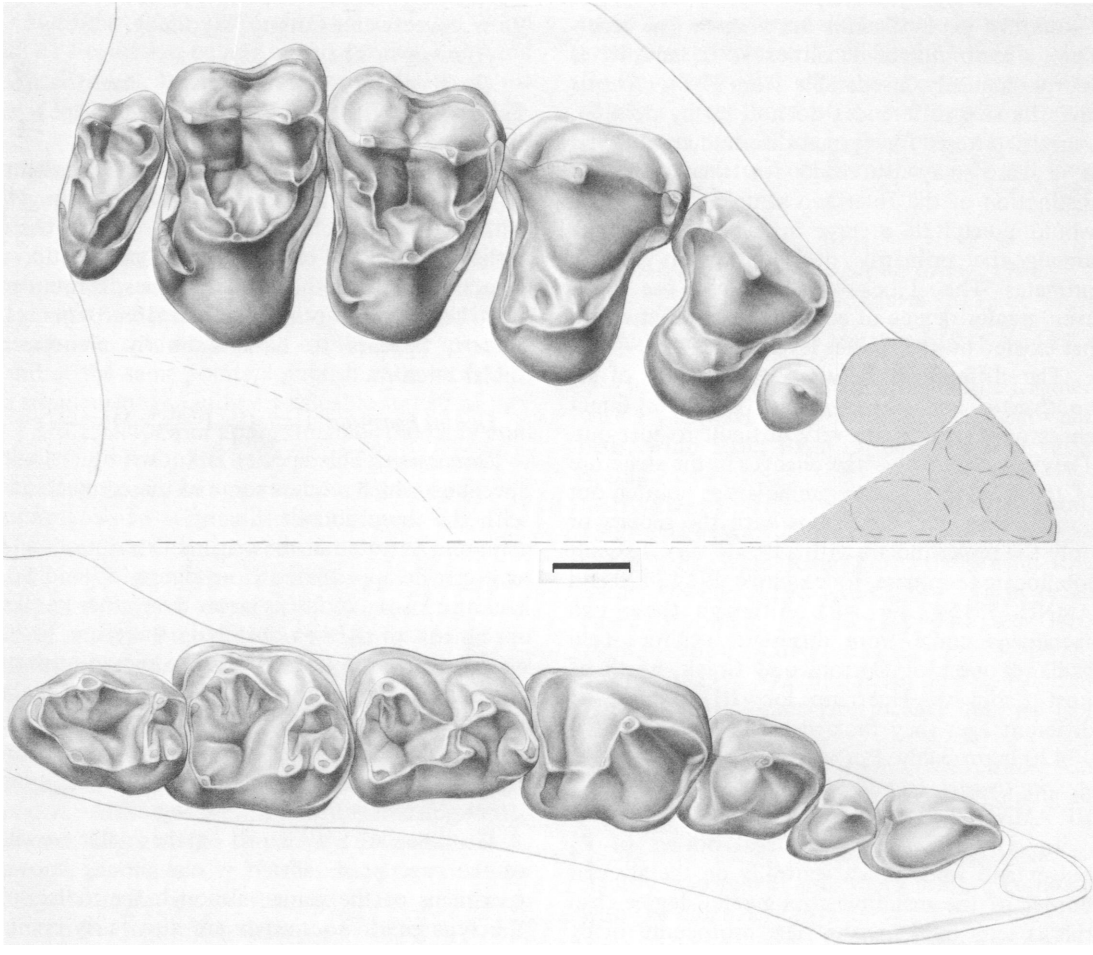


FIG. 46. *Absarokius abotti*, right upper (P^2-M^3) and left lower (C-M_3) dentitions based on YPM 18690 (upper dentition) and AMNH 12757, 12758, YPM 17473, 17476, and 27791 (lower dentition), Wasatchian of Wyoming and Colorado; occlusal views. Reconstruction shown by uniform stippling and broken lines. Scale represents 1 mm.

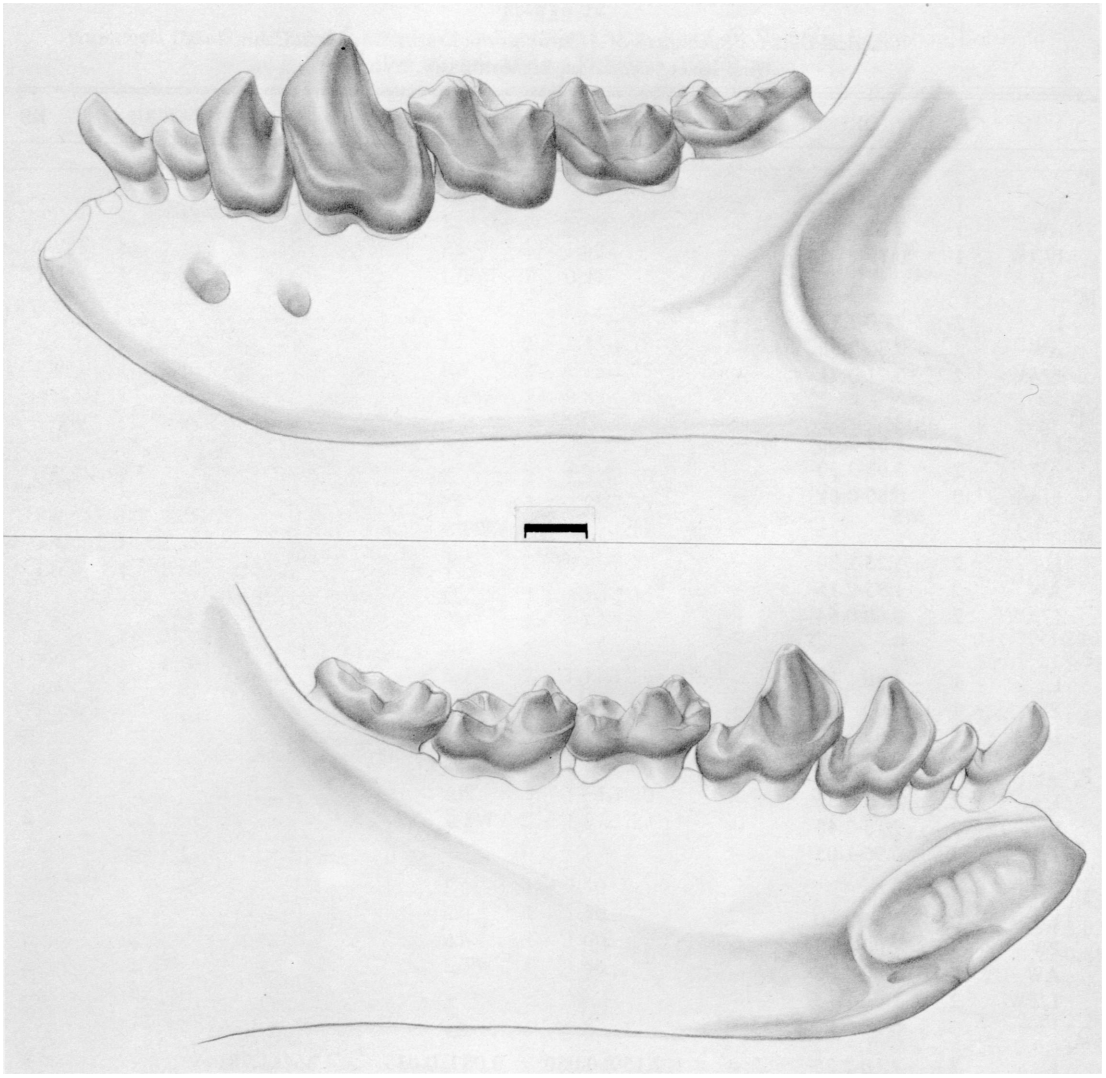


FIG. 47. *Absarokius abotti*, left horizontal ramus with C-M_3, based on AMNH 12757 and 12758, YPM 17473, 17476, and 27791, Wasatchian of Wyoming and Colorado; lateral (above), and medial (below) views, respectively. Scale represents 1 mm.

TABLE 11
Numerical Data for Specimens of *Absarokius noctivagus* from Lost Cabin Beds, Wind River Formation, Bighorn Basin, Wyoming

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P^4								
L	1	2.15	–	–	–	–	–	–
AW	1	2.85	–	–	–	–	–	–
L/AW	1	0.75	–	–	–	–	–	–
M^1								
L	2	2.00-2.13	–	–	–	–	–	–
AW	2	2.80-2.98	–	–	–	–	–	–
L/AW	2	0.71-0.71	–	–	–	–	–	–
M^2								
L	2	1.85-2.08	–	–	–	–	–	–
AW	2	3.05-3.50	–	–	–	–	–	–
L/AW	2	0.59-0.61	–	–	–	–	–	–
M^3								
L	2	1.25-1.30	–	–	–	–	–	–
AW	2	1.95-2.15	–	–	–	–	–	–
L/AW	2	0.60-0.64	–	–	–	–	–	–
P_3								
L	1	1.30	–	–	–	–	–	–
PW	1	2.00	–	–	–	–	–	–
L/PW	1	0.65	–	–	–	–	–	–
P_4								
L	2	2.25-2.35	–	–	–	–	–	–
PW	2	2.15-2.45	–	–	–	–	–	–
L/PW	2	0.96-1.05	–	–	–	–	–	–
M_1								
L	2	2.25-2.30	–	–	–	–	–	–
PW	2	2.00-2.20	–	–	–	–	–	–
AW	2	1.80-2.05	–	–	–	–	–	–
L/PW	2	1.05-1.13	–	–	–	–	–	–
M_2								
L	3	2.10-2.25	–	2.150±0.050	0.087±0.035	4.364±1.781	–	–
PW	3	1.90-2.10	−0.616	1.977±0.062	0.108±0.044	5.911±2.413	–	–
AW	3	1.90-2.00	−0.731	1.943±0.030	0.051±0.021	2.861±1.168	–	–
L/PW	3	1.00-1.18	–	1.091±0.053	0.092±0.038	0.151±3.736	–	–
M_3								
L	2	2.10-2.70	–	–	–	–	–	–
PW	2	1.50-1.50	–	–	–	–	–	–
AW	2	1.55-1.65	–	–	–	–	–	–
L/PW	2	1.40-1.80	–	–	–	–	–	–

TABLE 12
Numerical Data for *Absarokius* samples from Localities 1, 2, and 3 of the Huerfano Formation, Colorado
(For locality data see Robinson, 1966.)

	Locality 1		Locality 2		Locality 3	
	N	OR	*N*	OR	*N*	OR
P_4						
L	1	2.30				
PW	1	2.20				
L/PW	1	1.05				
M_1						
L	1	2.60				
PW	1	2.20				
AW	1	1.90				
L/PW	1	1.18				
M_2						
L	1	2.55				
PW	1	2.25				
AW	1	2.25				
L/PW	1	1.13				
M_3						
L	1	3.10				
PW	1	1.90				
AW	1	1.87				
L/PW	1	1.63				
	–	–				
	–	–				
	–	–				
	–	–				
	–	–				
	–	–				
	–	–				
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	–	–				
	–	–				
	–	–				
	–	–				
	–	–				
	–	–				
P_2						
L			1	1.45		
PW			1	1.60		
L/PW			1	0.91		
P_3						
L			2	1.45-1.70		
PW			2	1.75-1.75		
L/PW			2	0.83-0.97		
P_4						
L			2	2.33-2.50		
PW			2	2.25-2.35		
L/PW			2	0.99-1.11		
M_1						
L			2	2.20-2.35		
PW			2	1.87-1.95		
AW			2	1.75-1.85		
L/PW			2	1.13-1.26		
M_2						
L			3	2.15-2.20		
PW			3	1.75-2.00		
AW			3	1.65-1.90		
L/PW			3	1.07-1.23		
M_3						
L			1	2.40		
PW			1	1.50		
AW			1	1.60		
L/PW			1	1.60		
			–	–		
			–	–		
			–	–		
			–	–		
			–	–		
			–	–		
			–	–		
			–	–		
			–	–		
			–	–		
P_4						
L					1	2.15
PW					1	2.10
L/PW					1	1.02
M_1						
L					1	2.40
PW					1	2.00
AW					1	1.85
L/PW					1	1.20
M_2						
L					1	2.10
PW					1	2.10
AW					1	2.15
L/PW					1	1.00
M_3						
L					2	2.63-2.68
PW					2	1.70-1.75
AW					2	1.80-1.98
L/PW					2	1.53-1.55
P^3						
L					1	1.88
AW					1	2.13
L/AW					1	0.88
P^4						
L					2	2.30-2.45
AW					2	2.98-3.03
L/AW					2	0.77-0.81
M^1						
L					2	2.20-2.25
AW					2	3.08-3.25
L/AW					2	0.69-0.71
M^2						
L					1	2.15
AW					1	3.33
L/AW					1	0.65
P_3						
L					1	1.50
PW					1	1.28
L/PW					1	1.17

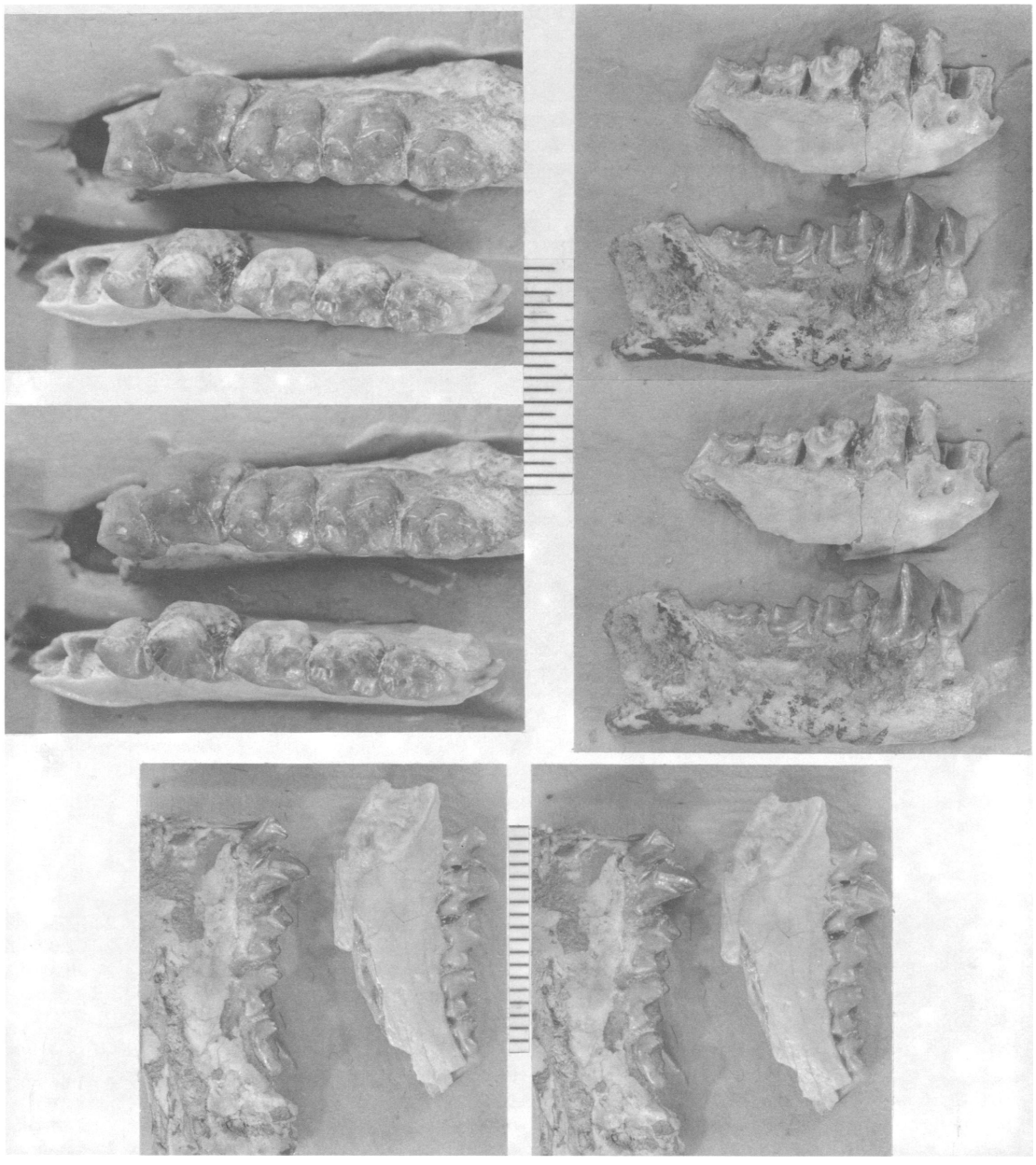


FIG. 48. *Absarokius noctivagus*, AMNH 15601, type, Lost Cabin beds, right mandible fragment with P_3-M_3 (top left, middle right, and bottom left). *Absarokius abotti*, UW 1644, Wasatch beds, Washakie basin, right P_3-M_3 (middle left, top right, and bottom right). Stereophotographs: lateral (left), and medial (right) views. Subdivisions on scales represent 0.5 mm.

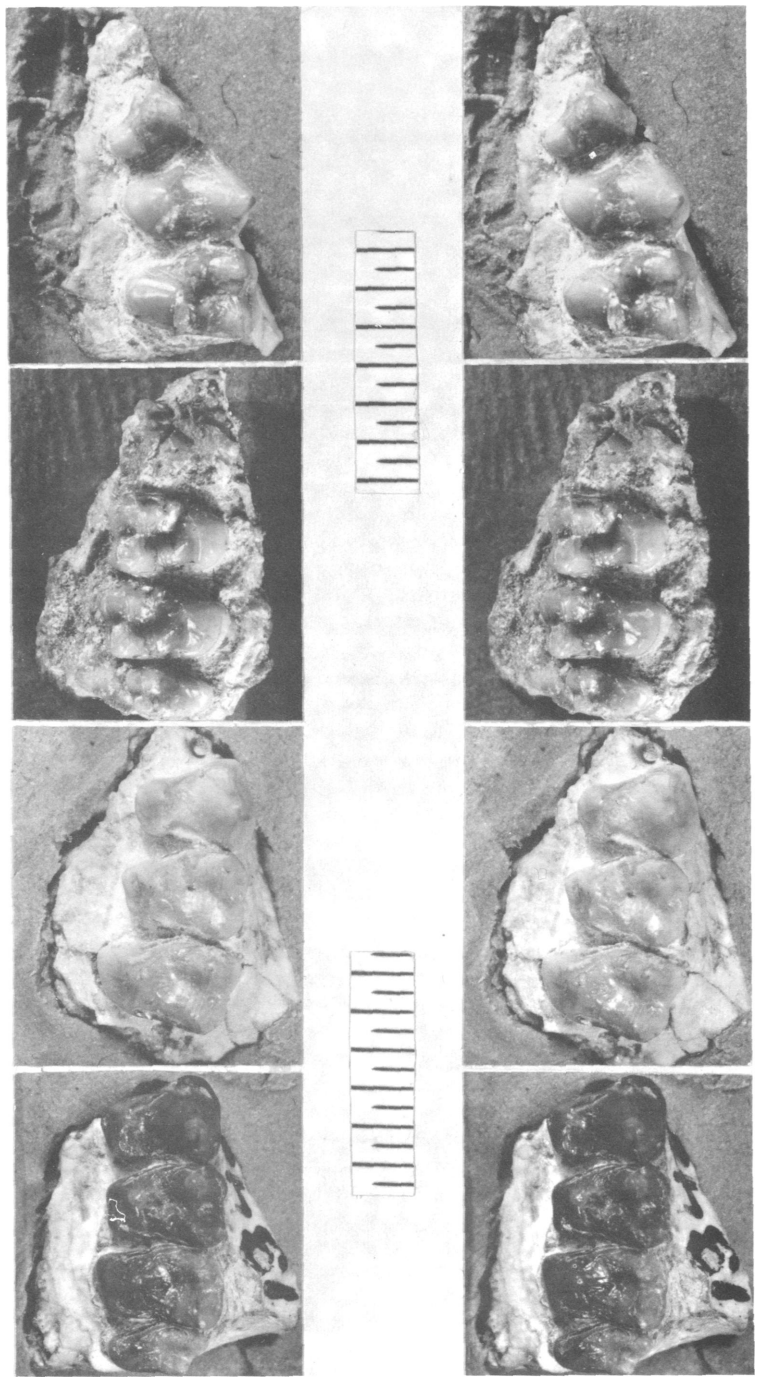


FIG. 49. *Absarokius noctivagus*, AMNH 55155, left P^3-M^1 (top); YPM 17488, right M^{1-3} (second from top); AMNH 55154, left P^4-M^2 (second from bottom); all from loc. III, Huerfano beds. *Absarokius abotti*, PU 13420, Lysite beds, left P^4-M^3 (bottom). Stereophotographs: occlusal views. Subdivisions on scales represent 0.5 mm.

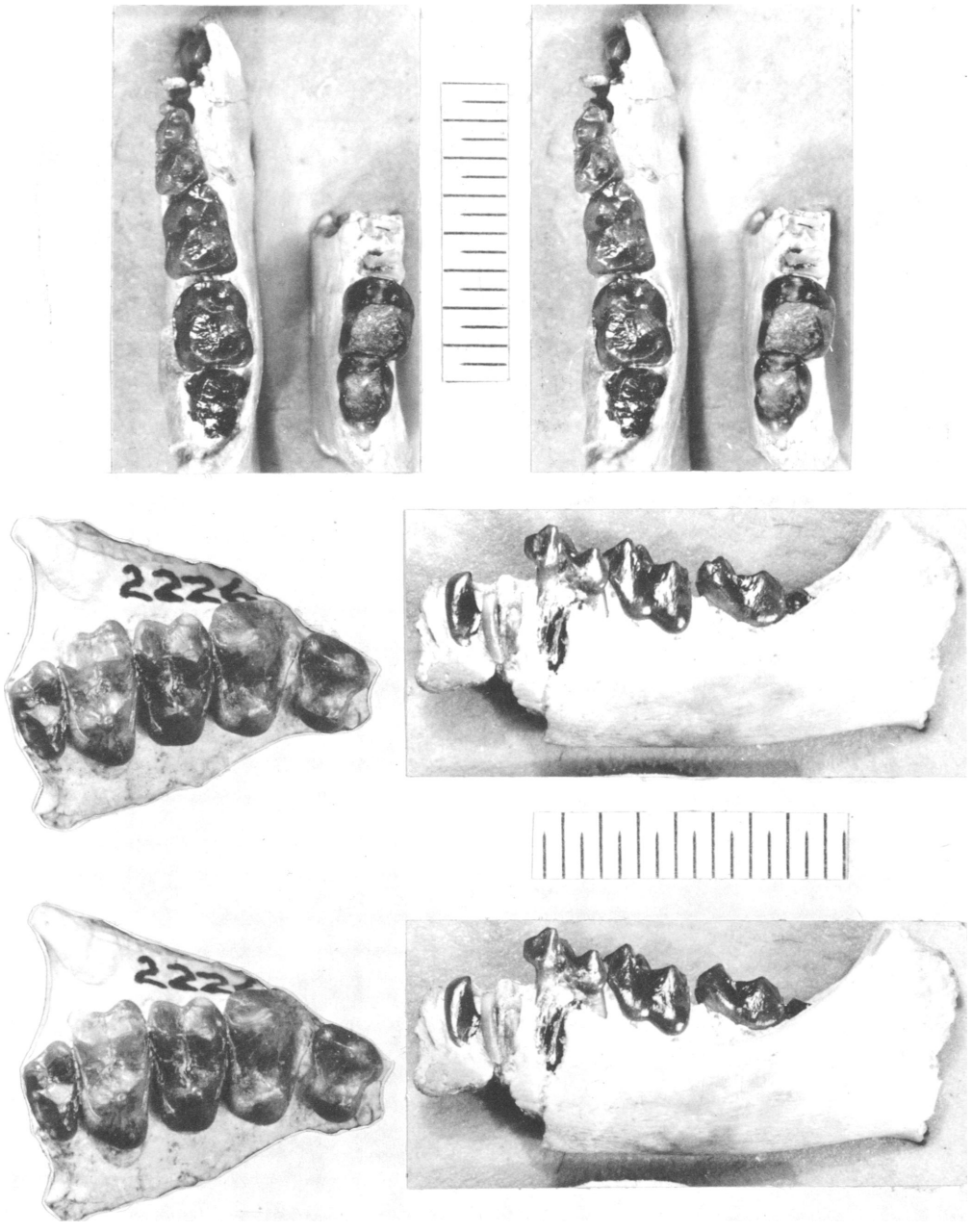


FIG. 50. *Absarokius noctivagus*, USNM 19198, left dP_3, dP_4, M_{1-3} (above left and below right); USNM 22264, right P^3-M^3 (below left); USNM uncatalogued specimen, right M_{2-3} (above right); all from Wasatch beds, upper Green River Basin. Stereophotographs: above and below left occlusal and below right lateral views. Subdivisions on scales represent 0.5 mm.

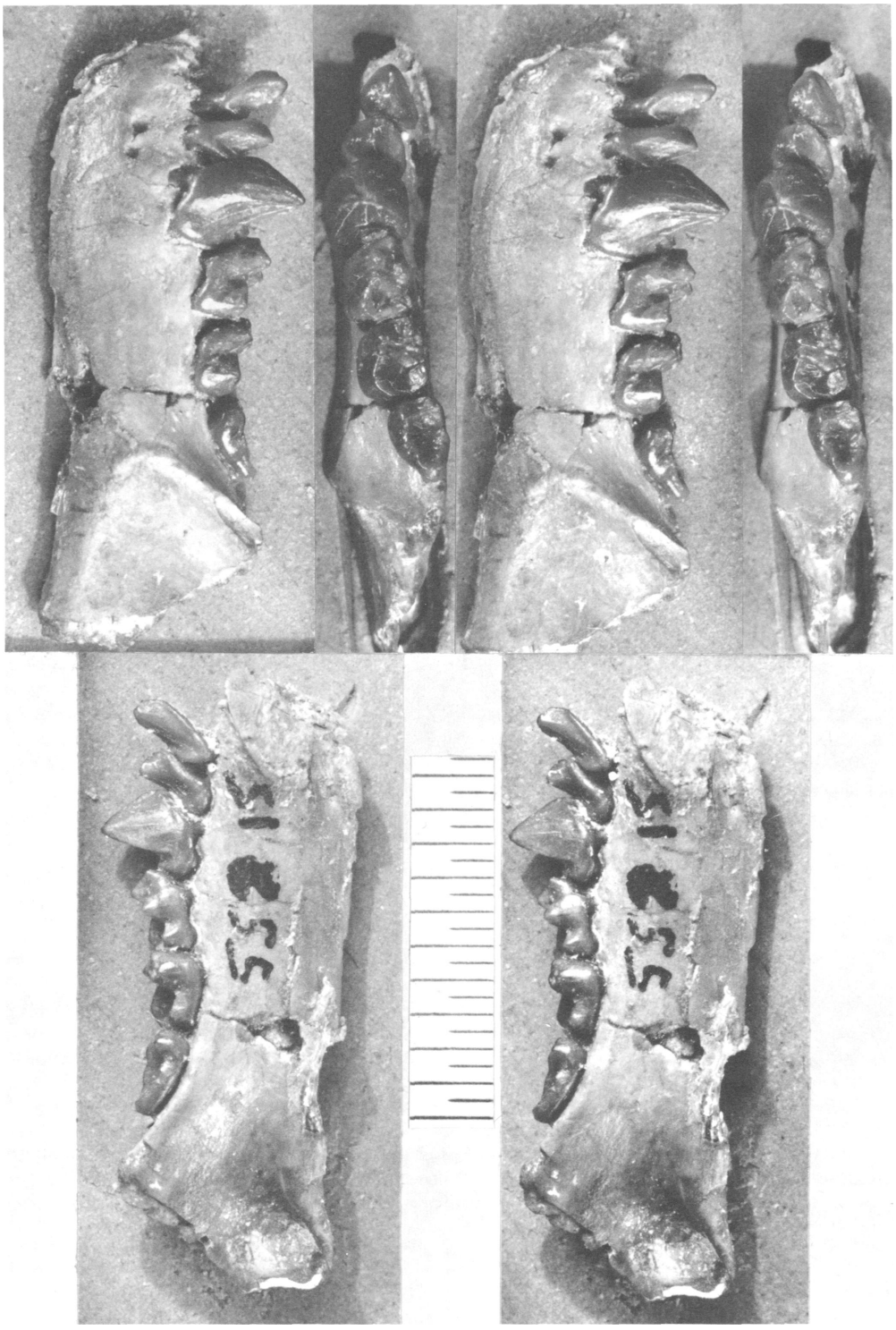


FIG. 51. *Absarokius noctivagus*, AMNH 55215, loc. II, Huerfano Formation, left P_2-M_3. Stereophotographs: above left lateral, above right occlusal, below medial views. Subdivisions on scale represent 0.5 mm.

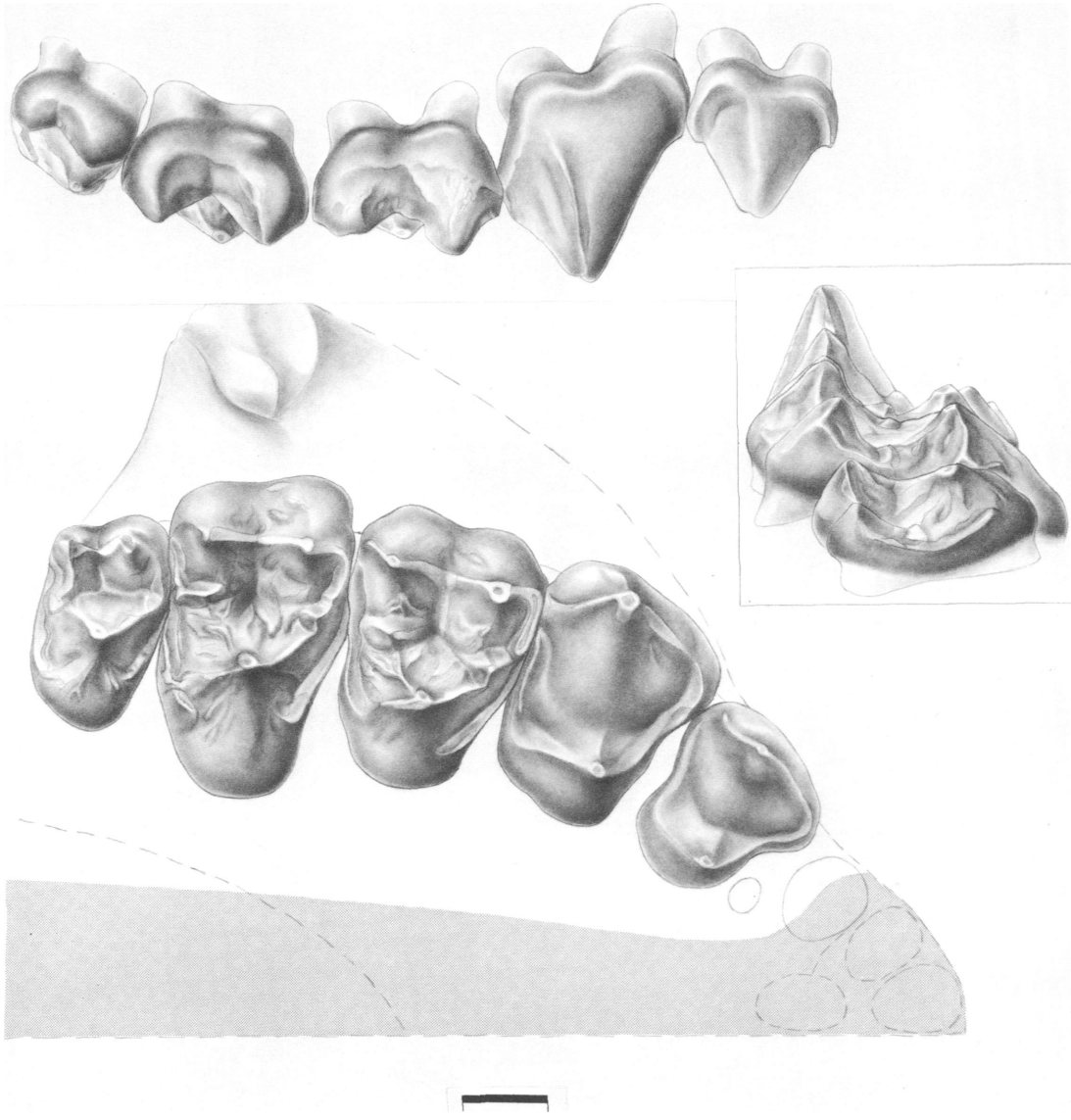


FIG. 52. *Absarokius noctivagus*, right P^3-M^3, based on AMNH 14663 and YPM 18686 and 18690, Wasatchian of Wyoming and Colorado; buccal (above), distal (right middle), and occlusal (below) views, respectively. Reconstruction shown by uniform stippling and broken lines. Scale represents 1 mm.

cracking open and crushing hard fruits, judgment on the exact nature of the cusp and the cutting edges must await the recovery of unworn specimens.

The two known molars of *A. witteri* have relatively broader talonid basins compared with the talonid width than those of *A. noctivagus* or *A. abotti*. For example, the ratio of the distance from the entoconid to the hypoconid over the width of the talonid is almost 0.8 in *A. witteri*,

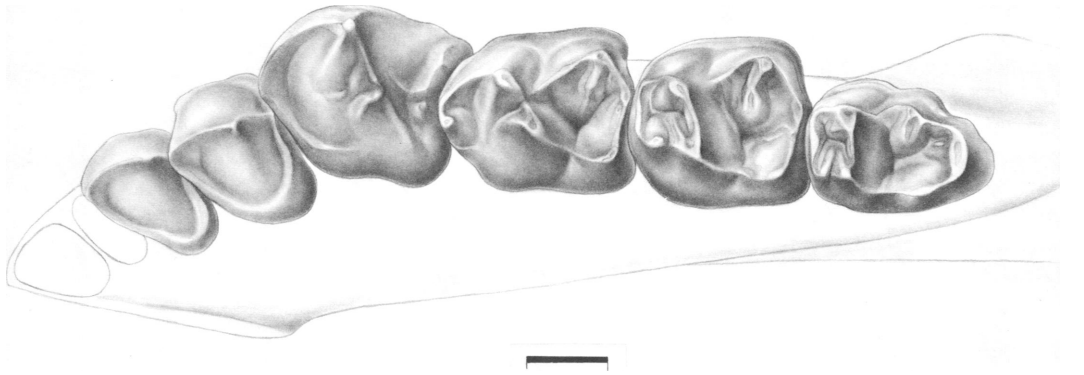


FIG. 53. *Absarokius noctivagus*, right C-M_3, based on AMNH 15601 and 55215, Wasatchian, Wyoming and Colorado; occlusal view. Scale represents 1 mm.

whereas in the Wasatchian species it is only over 0.5. *Absarokius abotti* and *A. noctivagus* appear to be advanced in this feature; the buccal sides of the talonids bulge in the manner characteristic of *Absarokius* yet in the youngest species of the genus, *A. witteri*, the relative width of the talonid basin compared with the width of the talonid is nearer to that seen in slightly modified early Tertiary primate lower molars. It is difficult to determine whether this feature of *A. witteri* is a secondary one, or merely representative of a different lineage of *Absarokius*, either a resident stock in the Washakie Basin or an immigrant into the basin. As with the talonid basins, the known trigonid basins are also more extensive transversely in *A. witteri* than in other known Wasatchian *Absarokius*.

In preparing the reconstruction of *A. witteri* (fig. 56) I have attempted to have P_3 drawn in relation to P_4 as those teeth occur in specimens of *A. abotti* and *A. noctivagus*. This could not be done without obvious distortions of the tooth. However, as unlikely as the position of P_3 may appear on the holotype, one must assume *faute de mieux* that in *A. witteri* P_3 is not so much under P_4 as in the Wasatchian species. The differences in the orientation of P_3, and also presumably of the canine, in *A. witteri* can be appreciated by comparing the figure of this species with those of *A. abotti* and *A. noctivagus*.

The exposed alveoli of M_1 of the type show that the lateral part of the roots were distinctly more robust than the medial ones. More robust buttressing of the lateral side, under the buccal side of the tooth, may be indicative of a special adaptation to withstand the forces of the masticatory stroke.

Numerical data in millimeters for the type specimen of *A. witteri*: LP_3, 1.63; PWP_3, 1.75; LP_3/PWP_3, 0.93; LP_4, 2.58; PWP_4, 2.75; LP_4/PWP_4, 0.94; LM_2, 2.63; PWM_2, 2.25; AWM_2, 2.28; LM_2/PWM_2, 1.17; LM_3, 2.80; PWM_3, 1.83; AWM_3; 2.03; LM_3/PWM_3, 1.53.

MCKENNAMORPHUS, NEW GENUS

Trogolemur: McKenna, 1960, p. 69.

Type Species. Mckennamorphus despairensis, new species.

Included Species. Type species only.

Geographical and Temporal Distribution. Wasatchian (early Eocene) of Colorado.

Generic Diagnosis. Differs from the contemporary and sympatric *Tetonius* in having an almost 100 percent more robust enlarged lower incisor. The premolars (only P_3 is known), the canine, and the small incisor have crowns with a relatively greater occlusal surface area than the homologous teeth in undoubted *Tetonius*, except possibly in *Tetonius? ambiguus* (Matthew, 1915). This genus differs from known *Trogolemur* in having the antemolar dentition much more tightly packed and consequently having an antemolar crown pattern relatively mesiodistally shorter and buccolingually wider than in *Trogolemur*.

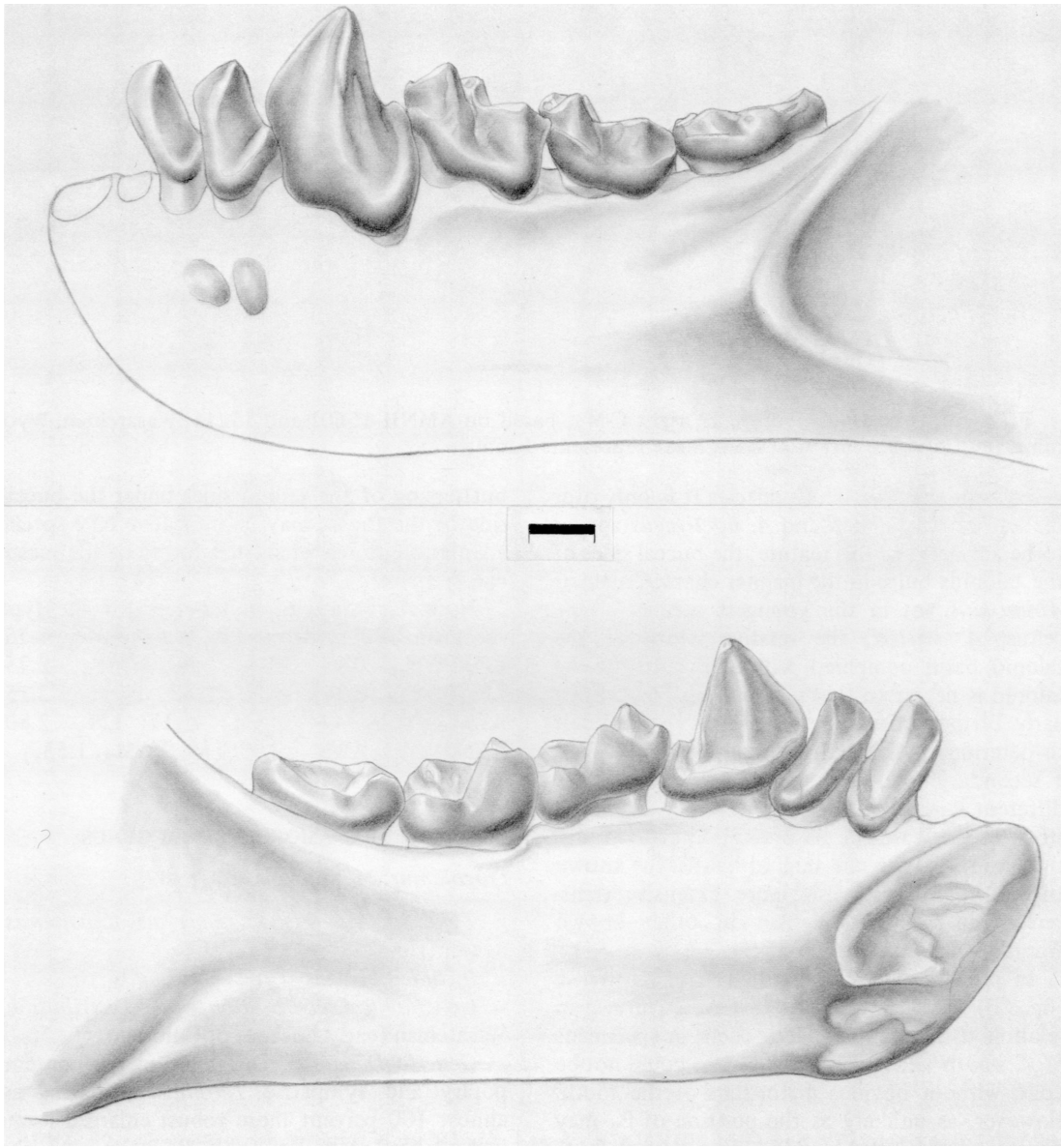


FIG. 54. *Absarokius noctivagus*, left horizontal ramus with C-M_3, based on AMNH 15601 and 55215, Wasatchian, Wyoming and Colorado; lateral (above) and medial (below) views, respectively. Scale represents 1 mm.

Discussion. This is a poorly known, and therefore problematical genus although its generic distinctness from the sympatric *Tetonius* is clear, as this was recognized by McKenna (1960, p. 69). From the symphyseal morphology and the little that is known of its cheek teeth it is clearly an omomyid primate and very likely an anaptomorphine related to *Tetonius*. Although the greatly enlarged incisor may suggest generic affinities with *Trogolemur*, the crown morphol-

gy of the antemolar teeth tend to preclude this, ıd the differences, noted under the diagnosis, ıdicate a clear generic distinction from *Trogo-mur* or any other known omomyid.

Etymology. Named for Dr. Malcolm C. cKenna, collector of the holotype, who saw its ɜneric distinctness from *Tetonius*; in recognition f his researches on Cretaceous and Tertiary ɜrtebrate faunas and mammalian evolutionary istory in general. The specific name is from the ɔovenance of the holotype from Despair uarry.

Adaptations. There are two highly significant ɜatures that are clearly discernible even on the ɜagmentary type specimen. The anterior incisor, ı, was nearly vertically implanted (unlike its orizontally placed homologue in *Trogolemur*) ıd was clearly the dominant feature of the ıandible. The crown was probably enormous ıd, judged by the teeth posterior to it, it robably had a mesiodistally running cutting dge, perhaps not unlike that of *Tetonius*. The ɜ, C, and P_3 distal to the root of I_1 are fairly niform in shape; they are well characterized by aving closely packed crowns each more wide ıan long. Their great relative width and nearly ontinuous cutting edges show these to be highly ınctional and not "reduced" teeth.

The large incisors are clearly a selective ɜsponse for the great stresses incurred by this ɔoth. This indicates a specialized activity prob-bly related to food procurement. To speculate n the nature of this activity is almost impossi-le, however, as only the crown of this tooth ɔould allow such attempts. Judging by the teeth ɨith crowns, I suspect that a mesiodistally riented rather than a transverse edge dominated ıis tooth. It was then probably unlike the ɔdent-like transverse cutting edges of the en-ırged incisors of the plesiadapid *Chiromyoides* r the lemuriform *Daubentonia* which do not ave the kind of cutting edges behind the ılarged incisor as does *Mckennamorphus*. Thus, erhaps the enlarged teeth of *Mckennamorphus* re not adaptations for gnawing wood like those f *Daubentonia* but rather for manipulation of articular kind(s) of hard fruits or seed pods. The road crowns of the antemolar teeth also suggest n active preparatory and perhaps even some ıasticatory function by these teeth.

The symphysis is sufficiently preserved to deserve comment. The dorsal part, best referred to as the superior transverse torus, is more of a semicircle than a shelf and it is anteroposteriorly the widest part of the symphysis. The great extent of the symphysis clearly reflects unusually great stresses, an inference in harmony with the presence of the enlarged incisor. The very large superior transverse torus perhaps reflects buttressing as a result of contralateral muscle input (?temporalis) into the function of the enlarged ipsilateral incisor.

This specialized genus is not likely to be either primarily insectivorous or folivorous. *Mckennamorphus* may be considered to have been frugivorous and omnivorous.

Mckennamorphus despairensis, new species
Figures 26, 28, 57

Trogolemur sp., McKenna, 1960, p. 69.

Type. UCMP 44055, right jaw fragment with root of enlarged I_1, of $I_{2(?)}$, C, P_3, and a fragment of P_4; from Despair Quarry (loc. V-5352 in McKenna, 1960) of Four Mile Creek area, Craig Quadrangle, Moffat County, Colorado.

Geographical and Temporal Distribution. Same as for the genus.

Hypodigm. The type only.

Specific Diagnosis. Only known species of the genus.

Dental Formula. $I\frac{1,2}{1,2}$; $C\frac{1}{1}$; $P\frac{?,3,4}{3,4}$; molars unknown.

Discussion. The type specimen was accurately described by McKenna (1960, p. 69) and therefore redescription is not necessary. McKenna has identified P_4 as M_1 and the description should be read accordingly.

This species, based on the type only, is obviously poorly known. The type specimen of *Tetonius*? *ambiguus*, AMNH 15072, from lower Gray Bull beds bears a P_3 which in many ways approaches that in *Mckennamorphus despairensis*, although the great size differences in the enlarged incisors clearly attest to species rank differences between the specimens. Relegation of *Tetonius*? *ambiguus* as a species of *Mckennamorphus* is possible, pending better material, but allocation of *M. despairensis* to *Tetonius* appears

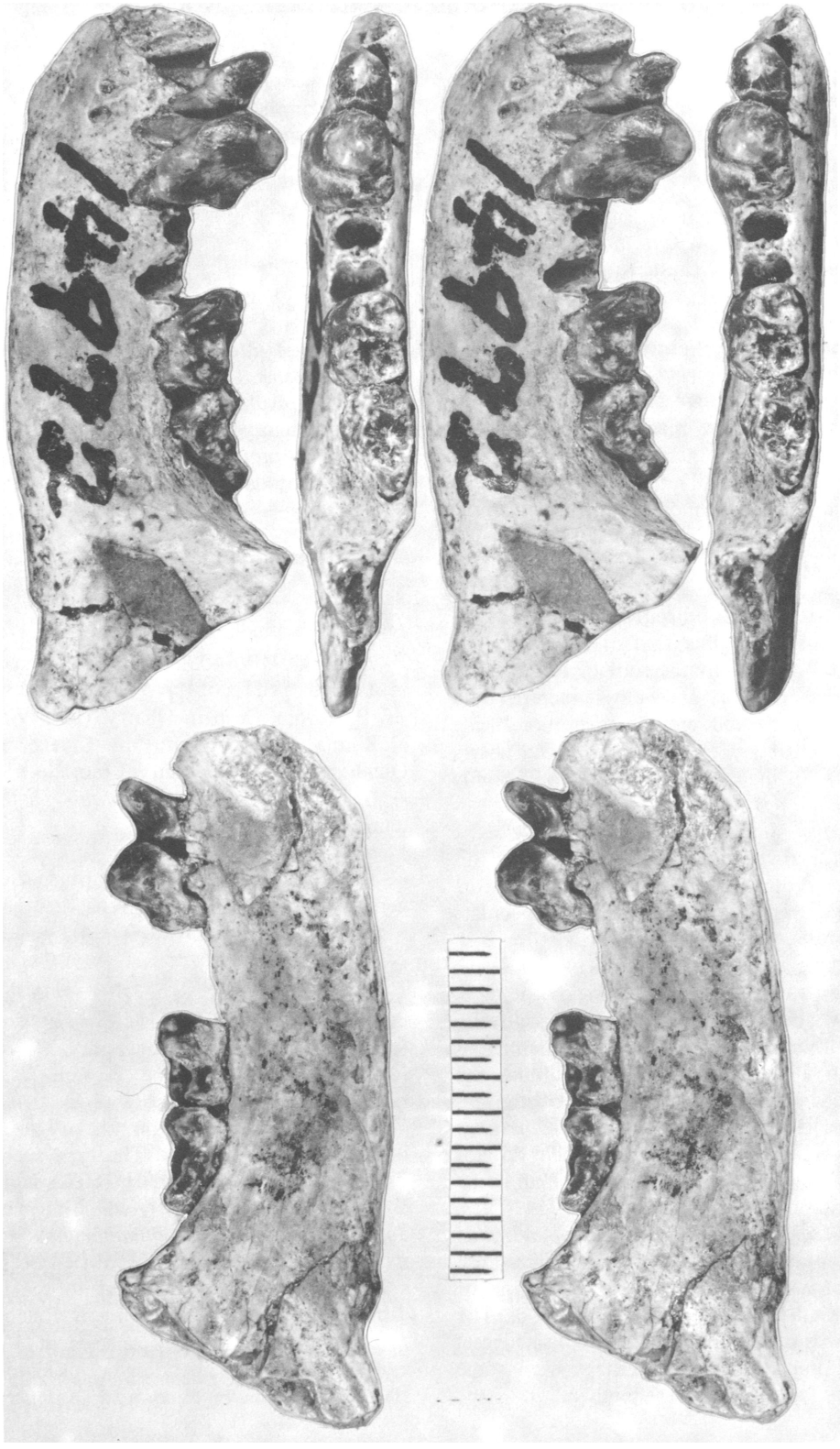


FIG. 55. *Absarokius witteri*, PU 14972, Cathedral Bluffs Tongue, Wasatch Formation, left P_{3-4} and M_{2-3}. Stereophotographs: above left lateral, above right occlusal, and below medial views. Subdivisions on scale represent 0.5 mm.

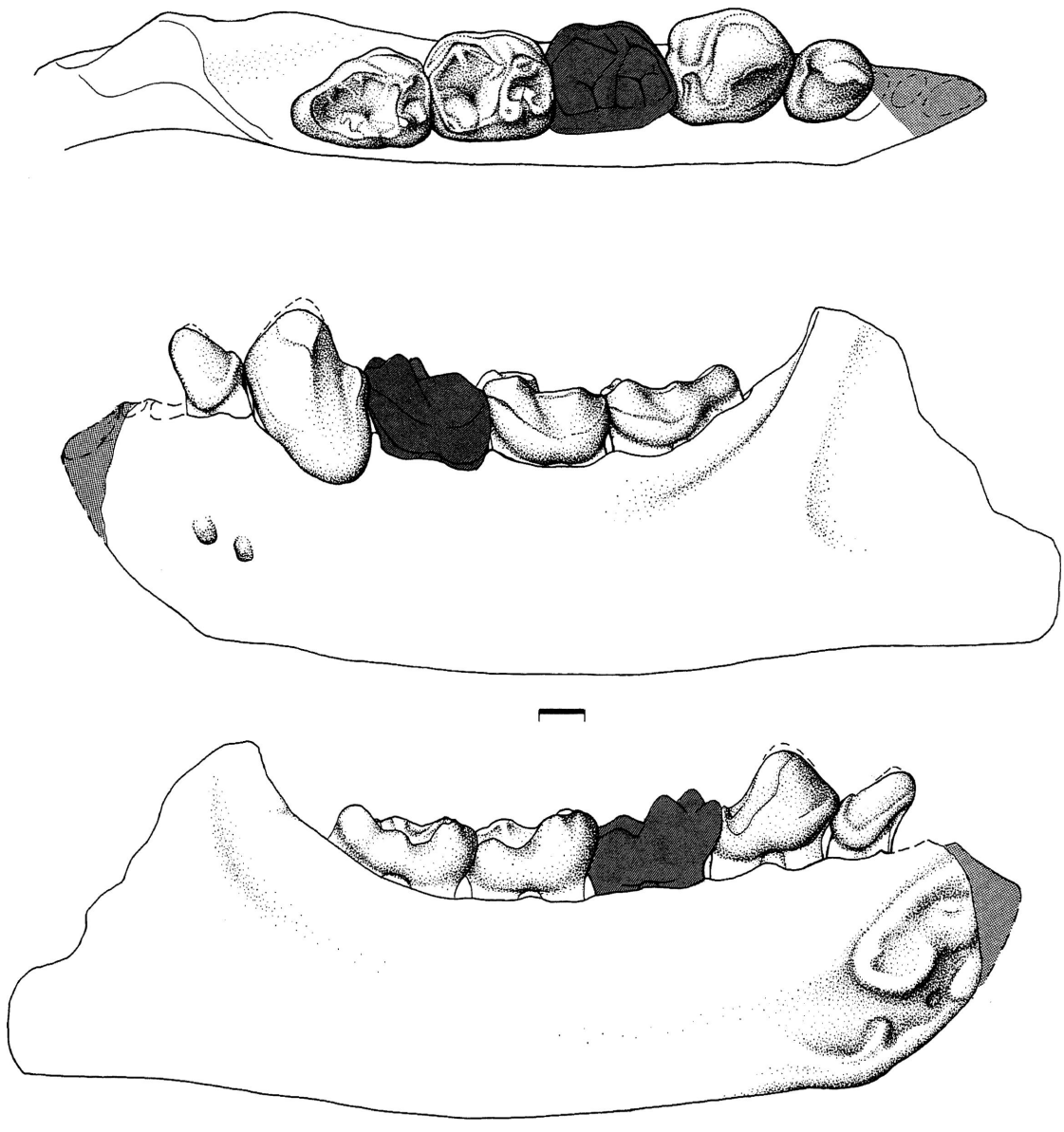


FIG. 56. *Absarokius witteri*, left horizontal ramus with P_{3-4} and M_{2-3}, M_1 is reconstructed, based on PU 14972, type, early Bridgerian of Wyoming; occlusal (above), lateral (middle), and medial (below) views, respectively. Reconstruction shown by uniform stippling, hatching, and broken lines. Scale represents 1 mm.

unlikely. The degree of incisor enlargement in the latter coupled with the changes in the antemolar crown patterns suggests a rather major shift in the feeding mechanism.

Measurements of the type of *M. despairensis*, in millimeters, are as follows: LP_3, 1.5; WP_3, 1.7; LP_2, 1.23; WP_2, 1.55; LI_2, 1.3; WI_2, 1.8; mesiodistal diameter of broken incisor root, 2.65;

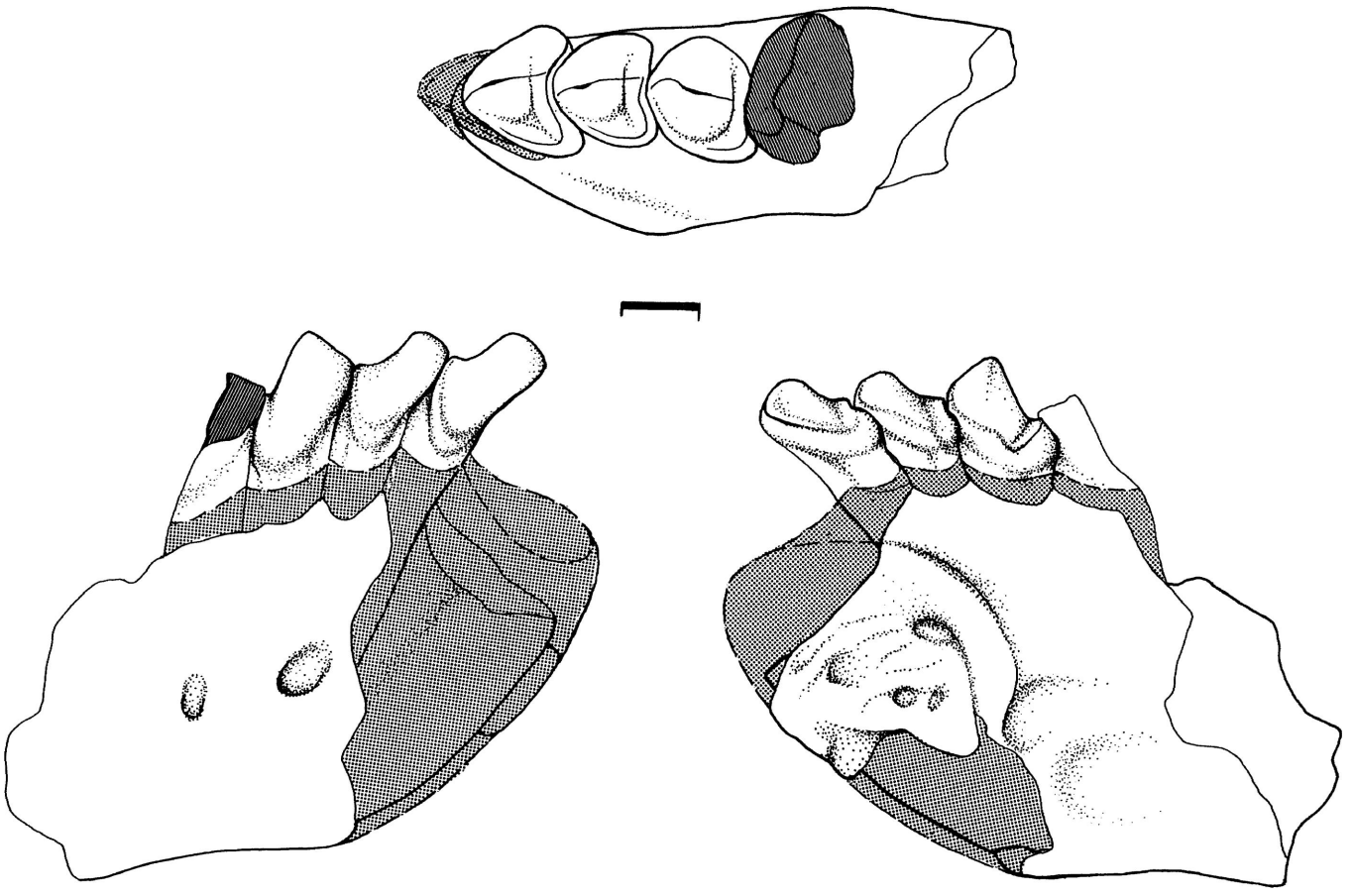


FIG. 57. *Mckennamorphus despairensis*, right jaw fragment with I_2-P_3 and fragment of P_4, based on UCMP 44055, type, Wasatchian of Colorado; occlusal (above), lateral (below left), and medial (below right) views. Reconstruction shown by uniform stippling, hatching, and broken lines. Scale represents 1 mm.

buccolingual diameter of broken incisor root, 1.55; jaw depth under P_4, measured medially, 4.8.

TRIBE TROGOLEMURINI, NEW

Type Genus. Trogolemur Matthew, 1909.

Included Genera. Trogolemur only.

Tribe Diagnosis. Anaptomorphines that differ from all other taxa of the subfamily in having an extremely reduced canine (? or P_2) and relatively very long third molars. The first pair of incisors is extremely enlarged, extending under the molars, unlike in *Mckennamorphus* or in any other anaptomorphines in which the enlarged incisors are more vertically placed and extend only under the anterior premolars.

Discussion. Trogolemurinines are the most distinctive and in many ways morphologically the most derived among known anaptomorphines. This is taxonomically best expressed in recognizing a suprageneric category of tribal rank. The most significant arguments for the anaptomorphine ties of this group are the shallowness of the talonid basin and the basal inflation of trigonid cusps.

TROGOLEMUR MATTHEW, 1909

Trogolemur Matthew, 1909, p. 546.

Type Species. Trogolemur myodes Matthew, 1909.

Geographical and Temporal Distribution. Bridgerian to Uintan (medial to late Eocene) of Wyoming.

Generic Diagnosis. As for the tribe.

Discussion. As noted by Gazin (1958, p. 80) this genus is clearly an anaptomorphine. The major changes from a *Chlororhysis-* or *Anemorhysis*-like ancestry involved an increase in the relative size of the root of I_1, the loss of P_2, the loss of the anterior roots of P_3 and P_4, and a slight increase in the relative size of M_3 compared with M_{1-2}. This latter trait may be an ancestral character retained in *Trogolemur.*

Adaptations. Trogolemur is poorly known, yet the known hypodigm gives an adequate idea of the characteristic lower dentition and part of the mandible.

The anterior incisor is very enlarged and extends as far back as the talonid of M_2. The tooth behind it, presumably an I_2, was very small by comparison and its crown was tucked under the third tooth of the jaw, probably the canine. This tooth was greatly overlapped by P_3, this in turn by P_4, and the latter by M_1. The premolars, as the molars, are low crowned with an elongated paracristid and a metaconid on P_4. The molar row is relatively very long and the crowns are broad and extensive. Molar trigonids are relatively wide and long mesiodistally and the paraconids and metaconids are not so closely twinned as in either *Tetonius* or *Anaptomorphus.*

The symphysis on the holotype, although most of it is broken, is the best one known and is very long and extensive. It lay nearly parallel with the inferior edge of the mandible as, for example, in *Anemorhysis.* The anterior half of the mandible is very robust, clearly to accommodate the enlarged incisors. Three mental foramina, one quite large, are present under P_4 and M_1. This latter may be of some significance for the physiology of the teeth, probably of the incisor. Continuous growth for the enlarged incisor is a possibility.

Trogolemur myodes was an extremely tiny mammal, with a skull probably barely exceeding 2 cm. in length! This very small size renders interpretations of the known morphology an additionally difficult task, as feeding habits of smaller living mammals are much more poorly known than larger ones. *Microcebus* and *Cebuella* are the only living primates in the size range of *Trogolemur* and their dental proportions show little adaptational similarity to those of this anaptomorphine.

A few general remarks, however, can be made of the available evidence. The open M_1 trigonids and talonids of the molars and the crowns of the antemolar teeth appear to have maximized the cutting edges. Judged from the conformation of the cheek teeth the large incisor was probably also a long-edged cutting tooth, but at any rate a tooth on which considerable stresses were incurred. The large M_3 talonid, relatively the largest among known omomyids, was of obvious significance for food processing in *Trogolemur.* A large M_3 talonid has come to be associated with extremes of some form of phytophagous rather than zoophagous diet. Thus it is possible that the combination of very large incisor, well-developed

cutting edges on the cheek teeth, and a relatively large M_3 talonid may reflect a diet in which food procurement was primarily dependent on prolonged incisor use and efficient slicing by the cheek teeth. Without more evidence from specimens, comparative occlusal studies of the kind advocated by Seligsohn and Szalay (In press) are not possible. Some specialized form of frugivory coupled with gum, resin, grub, and insect eating must suffice as a preliminary hypothesis for the diet of *Trogolemur*.

Trogolemur myodes Matthew, 1909
Figures 58, 59

Trogolemur myodes Matthew, 1909, p. 546.

Type. AMNH 12599, right mandible fragment with root of I_1, and P_2-M_3, collected from Bridger B beds, 6 miles south of Granger, Bridger Basin, Wyoming.

Hypodigm. The type and YPM 13523, from the Henry's Fork loc., Bridger beds, Wyoming.

Geographical and Temporal Distribution. Bridgerian (medial Eocene) of Wyoming.

Specific Diagnosis. Only known species of the genus.

Dental Formula. $I\frac{1,2}{1,2}$; $C\frac{1}{1}$; $P\frac{?,3,4}{3,4}$; $M\frac{1,2,3}{1,2,3}$.

Discussion. See under generic discussion.

Numerical data in millimeters for the type specimen of *Trogolemur myodes* is as follows: LM_3, 1.97; PWM_3, 1.20; AWM_3, 1.25; LM_2, 1.62; PWM_2, 1.50; AWM_2, 1.47; LM_1, 1.75; PWM_1, 1.27; AWM_1, 1.25; LP_4, 1.40; WP_4, 1.20; LP_3, 0.95; WP_3, 0.88; LP_2, 0.70; WP_2, 0.70.

Trogolemur sp.

?*Trogolemur* sp. Robinson, 1968, p. 324.

Two isolated teeth from Badwater Creek loc. 5a (CM 15066 and UCM 26043) were referred to ?*Trogolemur* sp. by Robinson (1968). I believe this allocation is probably correct.

SUBFAMILY OMOMYINAE TROUESSART, 1879

Omomynae Trouessart, 1879, p. 225.
Omomyinae Wortman, 1904, p. 29.
Omomyidae Gazin, 1958, p. 47.

Included Taxa. Tribe Omomyini Trouessart, 1879, tribe Washakiini new, tribe Uintaniini, new, tribe Utahiini, new, and tribe Rooneyiini, new.

Geographical and Temporal Distribution. Wasatchian to Chadronian (early Eocene to early Oligocene) of western North America.

Subfamily Diagnosis. The Omomyinae are the most diversified and longest lasting subfamily and in many features they appear unquestionably quite primitive. Mastoid inflation, well developed, as far as it can be assessed, in the anaptomorphine *Tetonius* and extremely developed in the microchoerine *Necrolemur*, is only slightly advanced in the only known complete cranium of an omomyine, that of *Rooneyia*. At least in several members of the subfamily the trigonid crests are rather high and the cusps are not broadly based like those of anaptomorphines. Along with the generally low-crowned molars, uninflated trigon cusps, and relatively tall trigonid crests, the talonid basins of the early representatives tend to be deep. In omomyines, unlike in anaptomorphines except *Trogolemur*, M_3 tends to be mesiodistally longer than M_2 and the M_3 talonid somewhat more transverse.

Discussion. The omomyines, as understood in this monograph, make their first appearance in *Omomys minutus* during the medial Wasatchian (Lysitean), whereas the last known taxon of this category (*Macrotarsius montanus*) is early Oligocene (Chadronian) in age. As noted under the family discussion, omomyines are the most varied of the subfamilies of the Omomyidae, requiring the tribal subdivisions proposed to express this diversity.

TRIBE OMOMYINI TROUESSART, 1879

Omomynae Trouessart, 1879, p. 225.

Type Genus. Omomys Leidy, 1869.

Included Taxa. Subtribe Omomyina Trouessart, 1879, and subtribe Macrotarsiina Robinson, 1968.

Tribe Diagnosis. Omomyinae with a probably derived absence of a protocone fold, three premolars, and moderately enlarged first incisors. The taxa included in this tribe appear to be monophyletic.

Discussion. The two groups included in this tribe may be viewed as representatives of two minor levels of dental organization in which the more primitive group is more ancient and the ancestor to the younger and more derived one. Late Eocene-early Oligocene macrotarsiinans are most likely derived from early-medial Eocene omomyinans.

SUBTRIBE OMOMYINA TROUESSART, 1879

Type Genus. Omomys Leidy, 1869.

Included Taxa. The type genus and *Chumashius.*

Subtribe Diagnosis. Omomyinines with a continuous lingual cingulum on the upper molars and a moderately piercing anterior dentition, when known.

OMOMYS LEIDY, 1869

Omomys Leidy, 1869, p. 63.
Euryacodon Marsh, 1872, p. 223.
Palaeacodon Marsh, 1872, p. 224.
Washakius: Simpson, 1959, p. 155.

Type Species. Omomys carteri Leidy, 1869.

Included Species. The type species, *Omomys minutus* (Loomis, 1906), and *Omomys lloydi* Gazin, 1958.

Geographical and Temporal Distribution. Medial Wasatchian to Bridgerian (medial early Eocene to medial Eocene) of Wyoming and Utah.

Generic Diagnosis. Differs from most omomyines, except *Chumashius* and *Dyseolemur*, in having lingually continuous cingula on the upper molars. It differs from *Chumashius* in having relatively taller third and fourth premolars. Although pericones occur in other omomyines in addition to *Omomys*, this genus is very distinct in having large, pointed pericones on the mesiolingual portion of the broad lingual cingulum as well as an equally distinct true hypocone distolingually. Lack of a trace of a protocone-fold is possibly a specialization of *Omomys* separating this genus from most other omomyines, except the other omomyinines. Differs from *Dyseolemur* in having sharp-crested cusps, unlike the more bulbously constructed molar crowns of that genus.

Discussion. Gazin (1958) discussed the arguments by Wortman (1903) for the suggested validity of *Euryacodon* and *Palaeacodon.* As Gazin noted, no serious doubt exists that they may represent taxa other than *Omomys carteri.* The very large sample from the Bridger Formation, apparently all of it from the lower (A-B) beds, clearly represents *O. carteri.*

There are some indications from the numerical data of *Omomys* from the Powder Wash loc. (table 15) that more than one species is represented in that sample. Gazin (1958, p. 52) has recognized this and based *Omomys lloydi* (see below) on one of the smaller specimens. Judged from both size and morphology, *Omomys carteri* also appears to be present at that locality.

In attempting to determine which specimen belongs to which of the similar species of *Omomys* in the Powder Wash sample, separation by size appeared to be the only reliable criterion. Even this was only reliable on the extremes of the ranges, as it is difficult, if not impossible, to determine the correct taxonomic status of first and second molar specimens with measurements between the extremes.

The dental morphology of most Eocene tarsiiforms has often been compared with *Omomys*, as there is, I believe, a tacit assumption in the works of most students that the dental morphology of *Omomys* is primitive for both the family and for the order. The original description of *Teilhardina belgica* would illustrate this point as the dentally primitive European *T. belgica* was held to be a species of *Omomys* and then later an omomyid, *sensu stricto.* Comparisons of *Omomys carteri* with paromomyid primates and anaptomorphine omomyids such as *Teilhardina*, *Anemorhysis*, and *Tetonius* reveal that the molar morphology of *Omomys* is different from the above genera in lacking the extensive slope distolingual to the apex of the protocone, and the protocone-fold. Instead, unlike the anaptomorphines cited, the hypocone function is performed only by a hypocone formed on the postcingulum itself. The distinctive pericone is an advanced feature and the true hypocone on the postcingulum is very probably also a derived character.

The discussion under *Chumashius* is closely pertinent to the treatment of *Omomys.*

Adaptations. Omomys is a rather unusual omomyid in lacking a protocone-fold and in hav-

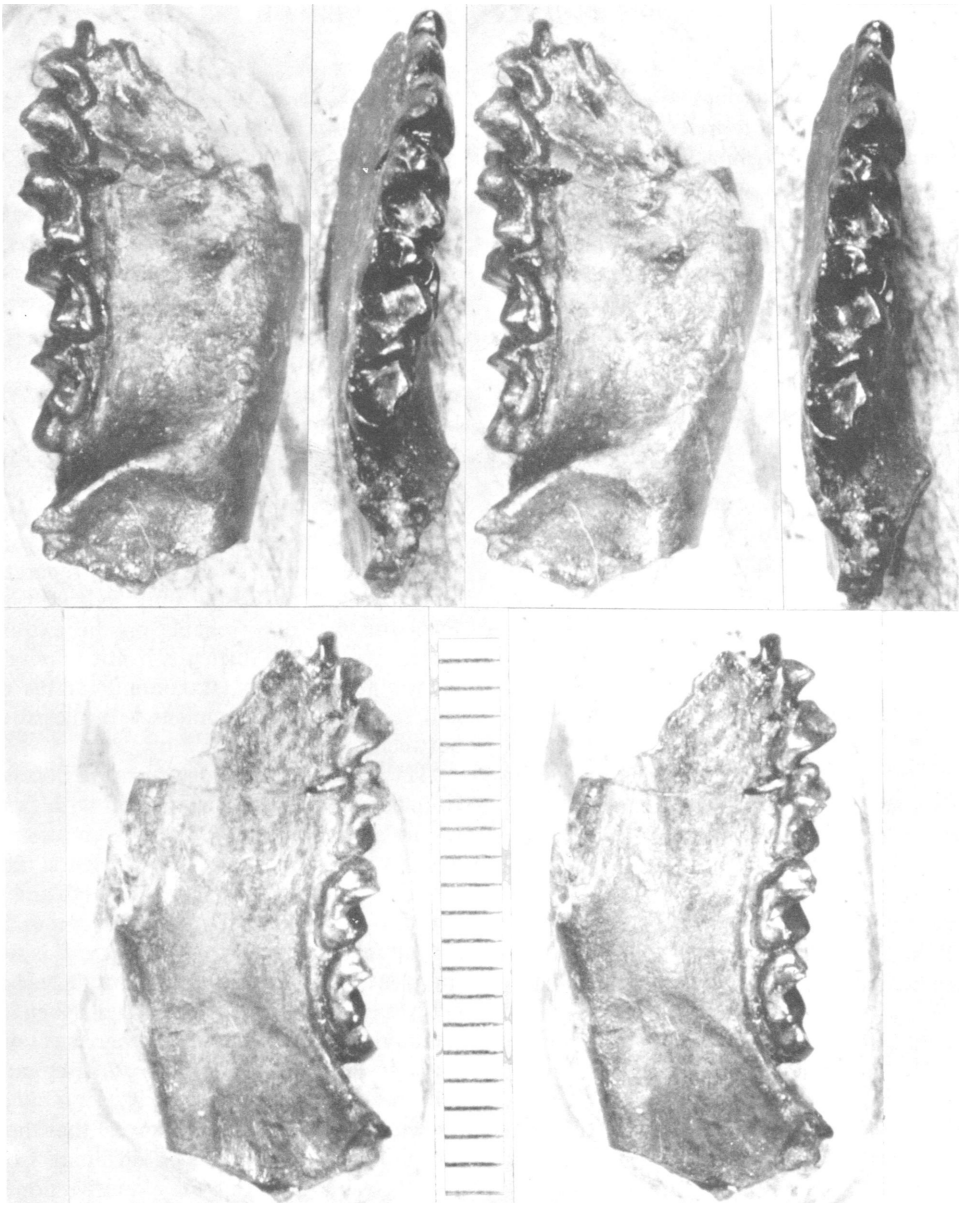


FIG. 58. *Trogolemur myodes*, AMNH 12519, Bridger beds, right C-M_3. Stereophotographs: above left lateral, above right occlusal, below medial views. Subdivisions on scale represent 0.5 mm.

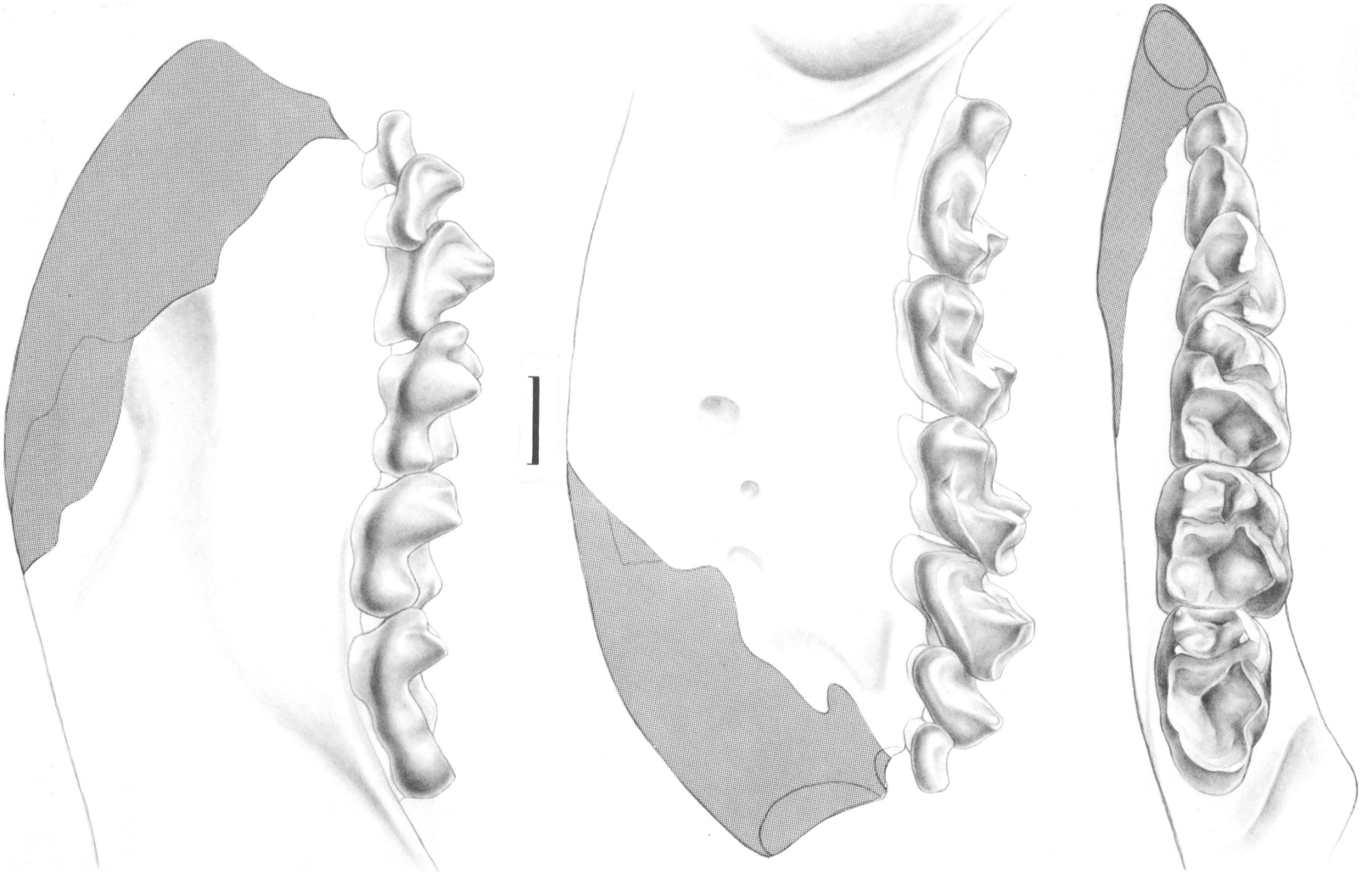


FIG. 59. *Trogolemur myodes*, right horizontal ramus with C-M_3, based on AMNH 12599, type, and YPM 13523, Bridgerian of Wyoming; occlusal (above), lateral (middle), and medial (below) views. Reconstruction shown by stippling and broken lines. Scale represents 1 mm.

ing a usually continuous lingual cingulum and a small cuspate hypocone budding off the latter.

The canines are considerably reduced in size and the incisors are moderately enlarged. The third premolars have rather robust and tall paracones and protoconids, respectively, an adaptation difficult to understand. It is an area of the tooth row that may have performed a role of piercing or puncturing in conjunction with the relatively small canines.

Perhaps another unusual feature of the known parts of this genus is the relatively long mandible. The second premolar is small, yet it is not sandwiched between the adjacent teeth. As far as one can tell of the meager sample of this region it has diastemata mesial and distal to it.

Under *Tetonius* I have contrasted some of the differences between the molar morphology of the former genus and *Omomys*. As I noted there, the dental evidence suggests a somewhat more orthal movement in occlusion than in *Tetonius* and perhaps this is indicative of a more vertical shear, often associated with zoophagy rather than with phytophagy. Species of *Omomys* were probably primarily insectivorous.

Omomys carteri Leidy, 1869
Figures 60-65; Table 13-15

Omomys carteri Leidy, 1869, p. 63.
Hemiacodon nanus Marsh, 1872, p. 213.
Hemiacodon pucillus Marsh, 1872, p. 222.
Omomys pucillus (Marsh, 1872) Wortman, 1904, p. 133.
Euryacodon lepidus Marsh, 1872, p. 223.
Palaeacodon vagus Marsh, 1872, p. 224.
Washakius insignis: Simpson, 1959, p. 155.

Type. ANS 10335, right mandible fragment with P_3, P_4, and M_2, collected from Bridger B beds, near Fort Bridger, Bridger Basin, Wyoming.

Hypodigm. The type and AMNH 11418-11423, 12041, 12042, 12600, 12603, 13033, 13036, 13038, 13059a, and 55673, YPM 11804, 11805, 11813, 11998, 13207-1, 13209, 13210-1, 13216-2, 13219-2, 13220-2, 13224-1, 13225-1, 13225-3, 13228-1, 13229-2, 16264, 16267, 16270, and 18854, all from various Bridger localities; many CM specimens from Powder Wash clearly belong to *O. carteri* but no certain allocation is feasible.

Geographical and Temporal Distribution. Bridgerian (medial Eocene) of Wyoming.

Dental Formula. $I\frac{1,2}{1,2}; C\frac{1}{1}; P\frac{2,3,4}{2,3,4}; M\frac{1,2,3}{1,2,3}$.

Discussion. There are no nomenclatorial problems concerning the described collections which have been allocated to this species. The most remarkable feature that can be noted about this taxon is the degree of morphological variation displayed by the upper molars from the Powder Wash quarry sample allocated to this species (fig. 66). The possibility exists, however, that several of these teeth represent *O. lloydi* of that quarry.

Omomys lloydi Gazin, 1958
Figures 66, 83; Tables 13, 15

Omomys lloydi Gazin, 1958, p. 52.

Type. CM 6417, left P_4-M_1, from the Green River Formation, Powder Wash loc. of the Carnegie Museum, about 2 miles southeast of Powder Springs, sect. 8, T. 7 S, R 25 E, Uinta Basin, Uinta County, Utah.

Hypodigm. The type and CM 6418, 6420, 17260, 17267, and 17304, all from Powder Wash.

Geographical and Temporal Distribution. Early Bridgerian (early medial Eocene) of Utah.

Specific Diagnosis. See discussion below.

Dental Formula. Probably the same as for *O. carteri.*

Discussion. There are as yet no reliable, clear-cut diagnostic features that would separate this species from *O. carteri.* The numerical data for the *Omomys* sample from the early Bridgerian Powder Wash loc. shows that the presence of another species in addition to *O. carteri* is very probable. The type and the additional specimens of the hypodigm are in the lower end of the size range for the sample. Therefore, they are likely to represent the species designated by Gazin as *Omomys lloydi* rather than *O. carteri.*

Omomys minutus (Loomis, 1906)
Figures 66, 67

Notharctus minutus Loomis, 1906, p. 283.
Omomys minutus (Loomis, 1906) Matthew, 1915, p. 463.

Type. AC 3365, right mandible fragment with M_{1-3}; collected from Wind River Formation, Lysite beds, Wind River Basin, Wyoming.

Hypodigm. Type only.

Geographical and Temporal Distribution.

Medial Wasatchian, (medial early Eocene) of Wyoming.

Specific Diagnosis. Smaller than either *Omomys carteri* or *O. lloydi.* Due to lack of an adequate sample the percentage of the size differences is not very meaningful. The mandible is distinctly shallower and more slender than those in *O. carteri* or *O. lloydi.*

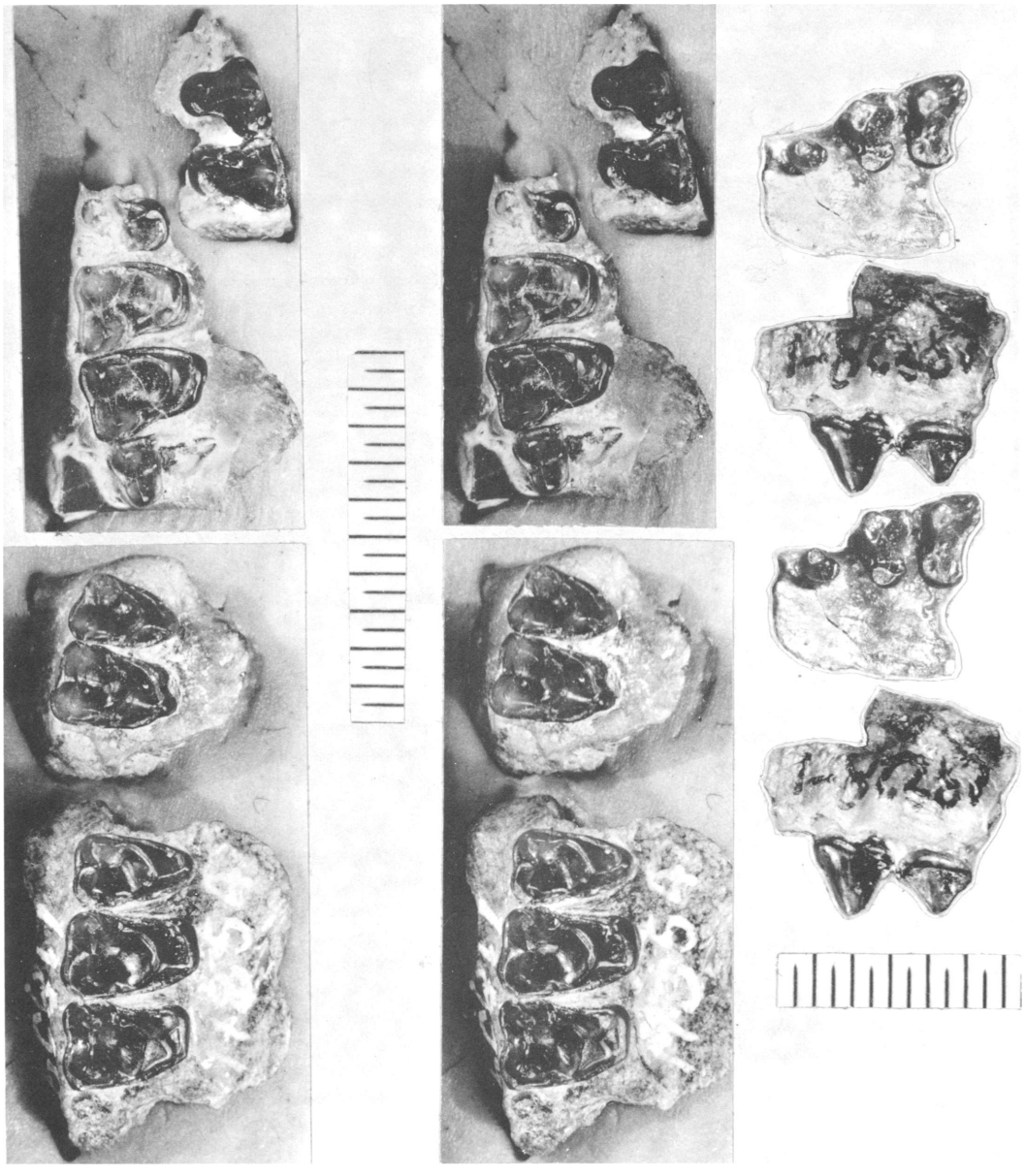


FIG. 60. *Omomys carteri*, YPM 13228-1, right P^4-M^3 (top left); YPM 13228-1, left P^{3-4} (top center and bottom right); YPM 11854, type of "*Palaeacodon vagus*," left M^{1-3} (bottom left); YPM 11813, type of "*Euryacodon lepidus*," left M^{2-3} (center left); and CM 6432, P^{2-4} (top right); all from Bridger beds. Stereophotographs: right below lateral, all other occlusal views. Subdivisions on scales represent 0.5 mm.

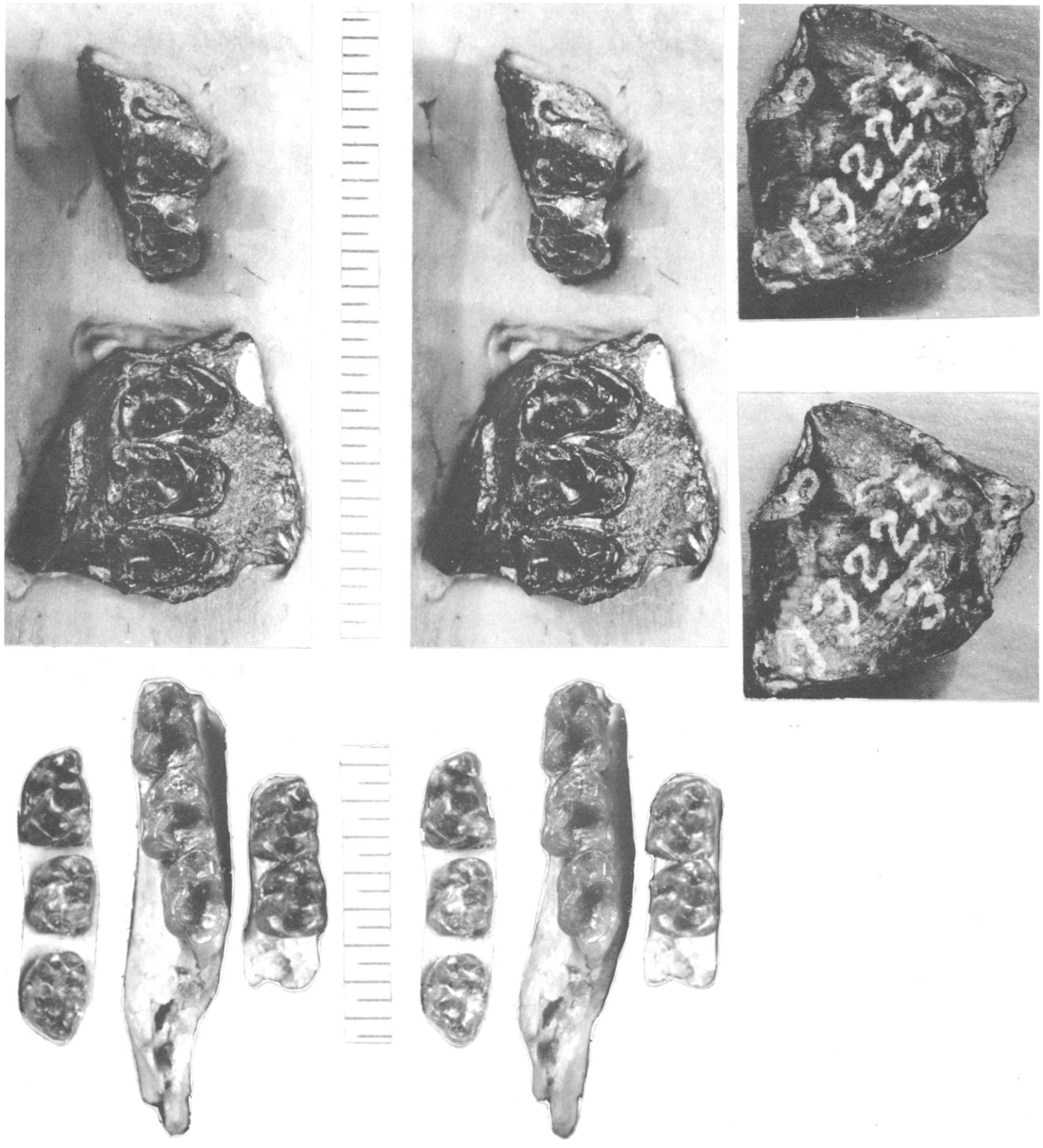


FIG. 61. *Omomys carteri*, YPM 13210-1, right P^{3-4} (above left); YPM 13225-3, right M^{1-3} (above right and second row left); AMNH 11418, left M_{1-3} (below center); all from Bridger beds. *Omomys lloydi*, CM 17267, left composite M_{1-3} (below left); CM 17304, left M_{1-2} (below right); both from Powder Wash, Green River beds. Stereophotographs: above right dorsal, all others occlusal views. Subdivisions on scales represent 0.5 mm.

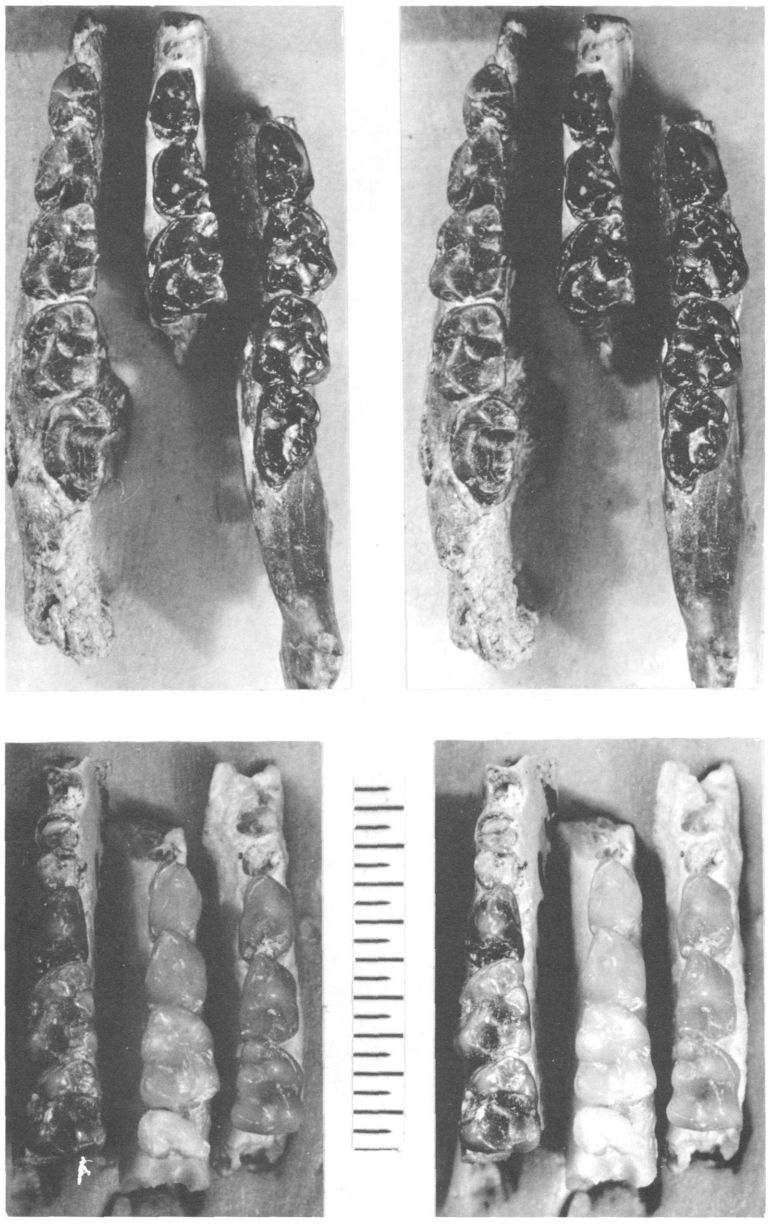


FIG. 62. *Omomys carteri*, AMNH 13033, left P_3-M_3 (above left); YPM 13219-2, left P_3-M_1 (above center); YPM 13219-2, right P_4-M_3 (above right); YPM 16264, left P_4-M_2 (below left); YPM 13207-1, right P_3-M_1 (below center); and YPM 13216-2, right P_3-M_1 (below right); all from Bridger beds. Stereophotographs: all occlusal views. Subdivisions on scale represent 0.5 mm.

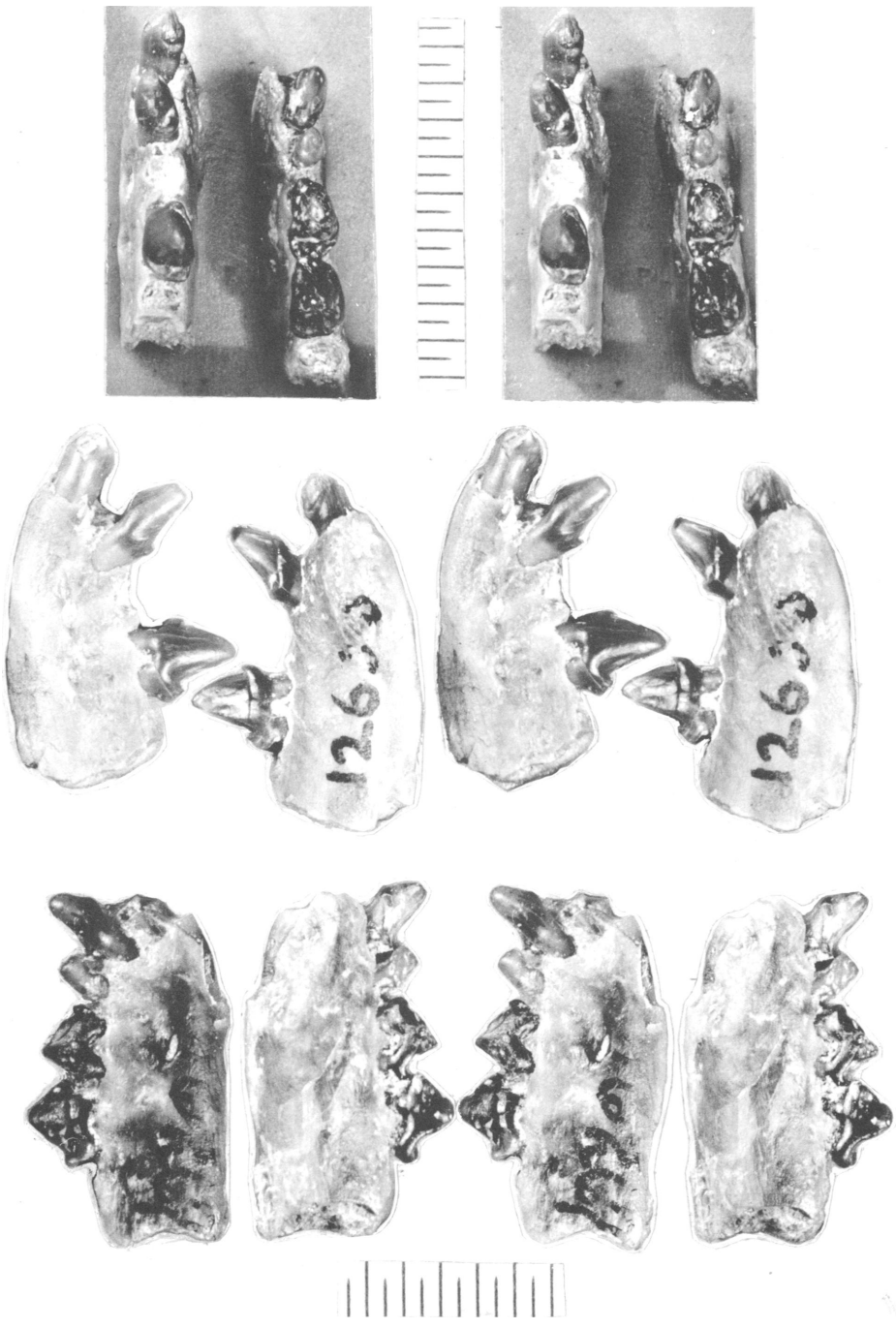


FIG. 63. *Omomys carteri*, AMNH 12600, left I_1, C, P_3 (above left and middle) and YPM 16267, right I_1-P_3 (above right and bottom); both from Bridger beds. Stereophotographs: above occlusal, middle left and bottom left lateral, and middle right and bottom right medial views. Subdivisions on scales represent 0.5 mm.

TABLE 13
Numerical Data for the Combined Sample of *Omomys* from the Powder Wash and Bridger Localities

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P^3								
L	3	1.49-2.15	–	1.847±0.192	0.333±0.136	19.548±7.980	–	–
AW	3	1.83-2.10	0.848	1.993±0.083	0.144±0.059	7.807±3.187	–	–
L/AW	3	0.81-1.05	–	0.923±0.068	0.118±0.048	13.891±5.671	–	–
P^4								
L	4	1.60-1.95	–	1.800±0.079	0.158±0.056	9.333±3.300	−0.632	−1.700
AW	4	2.26-2.80	0.696	2.465±0.118	0.236±0.084	10.191±3.603	1.385	2.005
L/AW	4	0.68-0.80	–	0.732±0.025	0.051±0.018	7.346±2.597	0.524	−0.634
M^1								
L	8	2.10-2.35	–	2.245±0.027	0.076±0.019	3.490±0.872	−0.783	1.132
AW	8	2.75-3.25	0.814	2.994±0.068	0.194±0.048	6.667±1.667	0.264	−1.449
L/AW	8	0.70-0.81	–	0.751±0.011	0.032±0.008	4.353±1.088	0.537	1.217
M^2								
L	12	2.00-2.27	–	2.153±0.031	0.108±0.022	5.119±1.045	−0.516	−1.456
AW	12	3.00-3.50	0.496	3.241±0.043	0.147±0.030	4.640±0.947	0.479	−0.062
L/AW	12	0.63-0.73	–	0.665±0.009	0.033±0.007	5.051±1.031	0.752	−0.391
M^3								
L	8	1.70-2.13	–	1.879±0.052	0.146±0.037	8.016±2.004	0.490	−0.529
AW	8	2.50-3.05	0.792	2.764±0.082	0.231±0.058	8.611±2.153	0.092	−2.028
L/AW	8	0.62-0.73	–	0.681±0.012	0.034±0.008	5.101±1.275	−0.454	−0.193
LC								
L	2	1.55-1.60	–	–	–	–	–	–
PW	2	0.95-1.10	–	–	–	–	–	–
L/PW	2	1.41-1.68	–	–	–	–	–	–
P_3								
L	17	1.60-2.25	–	2.061±0.035	0.146±0.025	7.193±1.234	−1.930	5.936
PW	17	1.20-1.52	0.225	1.383±0.021	0.085±0.015	6.252±1.072	−0.041	−0.069
L/PW	17	1.14-1.67	–	1.494±0.030	0.124±0.021	8.425±1.445	−1.333	3.002
P_4								
L	32	1.75-2.45	–	2.140±0.032	0.181±0.023	8.544±1.068	−0.737	−0.269
PW	32	1.30-1.90	0.256	1.570±0.022	0.122±0.015	7.810±0.976	0.457	0.710
L/PW	32	1.08-1.60	–	1.369±0.024	0.134±0.017	9.865±1.233	−0.261	−0.606
M_1								
L	34	2.03-2.70	–	2.424±0.028	0.162±0.020	6.741±0.817	−0.693	0.400
PW	34	1.63-2.10	0.339	1.850±0.020	0.118±0.014	6.435±0.780	0.471	−0.745
AW	34	1.50-1.95	0.422	1.733±0.019	0.112±0.014	6.523±0.791	0.073	−0.601
L/PW	34	1.07-1.53	–	1.313±0.017	0.099±0.012	7.606±0.922	0.101	0.715
M_2								
L	39	1.97-2.90	–	2.321±0.032	0.197±0.022	8.543±0.967	0.436	1.031
PW	39	1.50-2.25	0.458	1.882±0.025	0.153±0.017	8.191±0.927	−0.057	0.125
AW	39	1.47-2.10	0.624	1.801±0.022	0.138±0.016	7.700±0.872	−0.140	0.166
L/PW	39	0.95-1.54	–	1.237±0.017	0.105±0.012	8.510±0.964	0.311	1.711

TABLE 13–(*Continued*)

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
M_3								
L	22	2.00-3.05	–	2.604±0.053	0.250±0.038	9.725±1.466	–0.586	0.719
PW	22	1.24-1.90	0.877	1.591±0.034	0.161±0.024	10.235±1.543	–0.374	0.109
AW	22	1.26-1.95	0.832	1.626±0.034	0.161±0.024	10.033±1.513	–0.107	1.338
L/PW	22	1.52-1.81	–	1.639±0.018	0.083±0.012	5.101±0.769	0.651	–0.081

TABLE 14
Numerical Data for Specimens of *Omomys carteri* from Bridger Beds

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P^3								
L	2	1.90-2.15	–	–	–	–	–	–
AW	2	2.05-2.10	–	–	–	–	–	–
L/AW	2	0.90-1.05	–	–	–	–	–	–
P^4								
L	3	1.75-1.95	–	1.867±0.060	0.104±0.042	6.041±2.466	–	–
AW	3	2.35-2.80	0.474	2.533±0.136	0.236±0.096	10.105±4.125	–	–
L/AW	3	0.68-0.80	–	0.740±0.034	0.059±0.024	8.616±3.517	–	–
M^1								
L	4	2.25-2.35	–	2.287±0.024	0.048±0.017	2.224±0.786	0.855	–1.289
AW	4	2.95-3.25	0.987	3.075±0.066	0.132±0.047	4.571±1.616	0.864	–0.286
L/AW	4	0.72-0.76	–	0.744±0.008	0.017±0.006	2.370±0.838	–0.505	0.549
M^2								
L	7	2.00-2.25	–	2.186±0.036	0.094±0.025	4.478±1.197	–1.503	1.982
AW	7	3.20-3.50	0.296	3.286±0.042	0.111±0.030	3.491±0.033	1.405	1.705
L/AW	7	0.63-0.70	–	0.666±0.012	0.031±0.008	4.850±1.296	0.135	–1.770
M^3								
L	5	1.85-2.13	–	1.966±0.048	0.107±0.034	5.735±1.814	0.874	0.696
AW	5	2.75-3.05	0.272	2.910±0.066	0.147±0.047	5.321±1.683	–0.518	–3.175
L/AW	5	0.62-0.73	–	0.677±0.019	0.043±0.013	6.622±2.094	–0.031	–1.734
LC								
L	2	1.55-1.60	–	–	–	–	–	–
PW	2	0.95-1.10	–	–	–	–	–	–
L/PW	2	1.41-1.68	–	–	–	–	–	–
P_2								
L	1	1.10	–	–	–	–	–	–
PW	1	0.80	–	–	–	–	–	–
L/PW	1	1.37	–	–	–	–	–	–
P_3								
L	11	1.95-2.25	–	2.062±0.025	0.083±0.018	4.101±0.874	0.966	1.690
PW	11	1.20-1.50	0.682	1.375±0.026	0.086±0.018	6.408±1.366	–0.352	0.727
L/PW	11	1.38-1.63	–	1.502±0.021	0.070±0.015	4.742±1.011	–0.195	0.102

TABLE 14–(*Continued*)

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P_4								
L	20	1.90-2.40	–	2.187±0.026	0.118±0.019	5.460±0.863	−0.870	0.891
PW	20	1.40-1.90	0.360	1.592±0.027	0.123±0.019	7.803±1.234	0.808	0.539
L/PW	20	1.18-1.57	–	1.379±0.023	0.104±0.016	7.633±1.207	0.046	−0.873
M_1								
L	24	2.20-2.70	–	2.456±0.021	0.105±0.015	4.302±0.621	−0.149	1.161
PW	24	1.75-2.10	0.455	1.891±0.023	0.112±0.016	5.964±0.861	0.219	−1.100
AW	24	1.60-1.95	0.252	1.779±0.019	0.094±0.014	5.351±0.772	−0.079	−0.170
L/PW	24	1.13-1.43	–	1.302±0.014	0.071±0.010	5.506±0.795	−0.396	0.324
M_2								
L	21	2.00-2.90	–	2.374±0.039	0.177±0.027	7.554±1.166	0.763	3.457
PW	21	1.80-2.25	0.221	1.986±0.023	0.105±0.016	5.353±0.826	0.418	0.591
AW	21	1.70-2.10	0.573	1.890±0.022	0.100±0.015	5.327±0.822	0.206	−0.147
L/PW	21	0.95-1.41	–	1.198±0.021	0.095±0.015	8.060±1.244	−0.202	1.843
M_3								
L	10	2.50-3.05	–	2.735±0.057	0.180±0.040	6.730±1.505	0.233	−0.872
PW	10	1.50-1.90	0.863	1.708±0.035	0.109±0.024	6.567±1.468	−0.259	0.922
AW	10	1.60-1.95	0.702	1.733±0.041	0.129±0.029	7.636±1.707	0.956	−0.271
L/PW	10	1.52-1.70	–	1.602±0.018	0.057±0.013	3.653±0.817	0.211	−0.056

TABLE 15
Numerical Data for *Omomys* Specimens from Powder Wash

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P^2								
L	1	1.11	–	–	–	–	–	–
AW	1	0.75	–	–	–	–	–	–
L/AW	1	1.48	–	–	–	–	–	–
P^3								
L	1	1.49	–	–	–	–	–	–
AW	1	1.83	–	–	–	–	–	–
L/AW	1	0.81	–	–	–	–	–	–
P^4								
L	1	1.60	–	–	–	–	–	–
AW	1	2.26	–	–	–	–	–	–
L/AW	1	0.71	–	–	–	–	–	–
M^1								
L	4	2.10-2.29	–	2.202±0.040	0.080±0.028	3.847±1.360	−0.510	0.483
AW	4	2.75-3.25	0.683	2.912±0.114	0.229±0.081	8.342±2.949	1.811	3.380
L/AW	4	0.70-0.81	–	0.758±0.022	0.044±0.016	6.170±2.182	−0.093	0.657

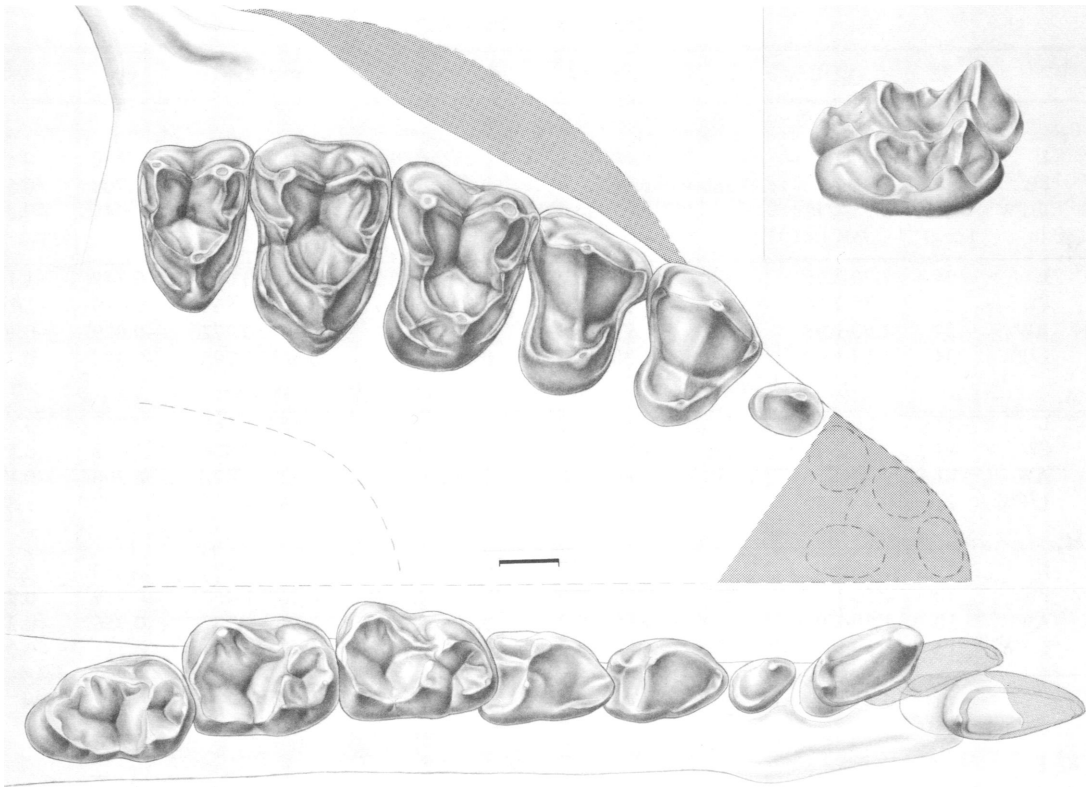


FIG. 64. *Omomys carteri*, right P^2-M^3 (above), based on AMNH 12041 and isolated, unnumbered specimens, I_1-M_3 (below), based on AMNH 12600 and 13033 and CM 8754 and 23499, Bridgerian of Wyoming and Colorado; above left and below occlusal and above right distal views. Reconstruction shown by uniform stippling. Scale represents 1 mm.

TABLE 15–(*Continued*)

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
M^2								
L	5	2.00-2.27	–	2.108±0.053	0.119±0.038	5.950±1.882	0.553	−1.821
AW	5	3.00-3.48	0.507	3.178±0.081	0.181±0.057	5.986±1.893	1.494	2.867
L/AW	5	0.63-0.73	–	0.664±0.017	0.039±0.012	6.162±1.949	1.637	3.077
M^3								
L	3	1.70-1.75	–	1.733±0.017	0.029±0.012	1.804±0.737	–	–
AW	3	2.50-2.53	−0.500	2.520±0.010	0.017±0.007	0.745±0.304	–	–
L/AW	3	0.67-0.70	–	0.688±0.008	0.014±0.006	2.270±0.927	–	–
P_3								
L	5	2.05-2.23	–	2.152±0.031	0.069±0.022	3.387±1.071	−0.606	0.114
PW	5	1.32-1.52	−0.063	1.396±0.045	0.100±0.032	7.533±2.382	0.652	−3.027
L/PW	5	1.38-1.67	–	1.548±0.054	0.122±0.038	8.257±2.611	−0.774	−1.398
P_4								
L	9	1.80-2.45	–	2.142±0.073	0.220±0.052	10.533±2.483	−0.508	−0.672
PW	9	1.30-1.70	0.117	1.526±0.042	0.127±0.030	8.536±2.012	−0.160	−0.036
L/PW	9	1.08-1.60	–	1.411±0.055	0.164±0.039	11.926±2.811	−1.049	1.028

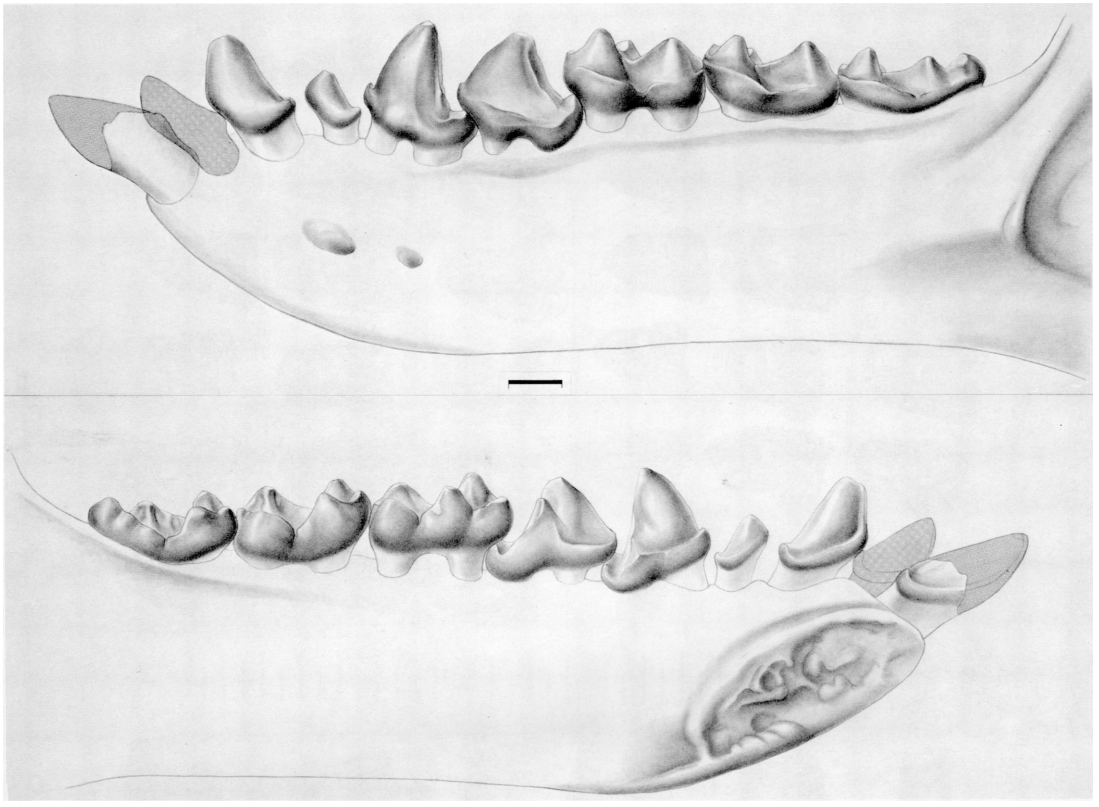


FIG. 65. *Omomys carteri*, left horizontal ramus with I_1-M_3, based on AMNH 12600 and 13033 and CM 8754 and 23499, Bridgerian of Wyoming and Colorado; lateral (above) and medial (below) views. Reconstruction shown by uniform stippling. Scale represents 1 mm.

TABLE 15–(*Continued*)

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
M_1								
L	8	2.03-2.70	–	2.402±0.084	0.238±0.060	10.237±2.559	−0.335	−1.274
PW	8	1.73-1.90	−0.647	1.767±0.019	0.054±0.014	3.177±0.794	2.639	7.237
AW	8	1.58-1.73	0.322	1.640±0.018	0.052±0.013	3.276±0.819	0.800	−0.394
L/PW	9	1.07-1.53	–	1.363±0.057	0.160±0.040	12.134±3.033	−0.785	−0.017
M_2								
L	16	1.97-2.75	–	2.277±0.053	0.211±0.037	9.409±1.663	0.384	0.158
PW	16	1.50-1.98	0.557	1.761±0.027	0.109±0.019	6.310±1.116	−0.586	1.729
AW	16	1.47-1.81	0.664	1.702±0.025	0.100±0.018	5.957±1.053	−1.240	0.765
L/PW	16	1.16-1.54	–	1.294±0.025	0.098±0.017	7.729±1.366	0.902	1.488
M_3								
L	10	2.00-2.92	–	2.480±0.088	0.277±0.062	11.457±2.562	−0.301	−0.015
PW	10	1.24-1.67	0.857	1.489±0.045	0.143±0.032	9.834±2.199	−0.644	−0.737
AW	10	1.26-1.70	0.830	1.533±0.045	0.143±0.032	9.581±2.142	−1.110	0.400
L/PW	10	1.53-1.81	–	1.666±0.030	0.095±0.021	5.875±1.314	0.422	−0.861

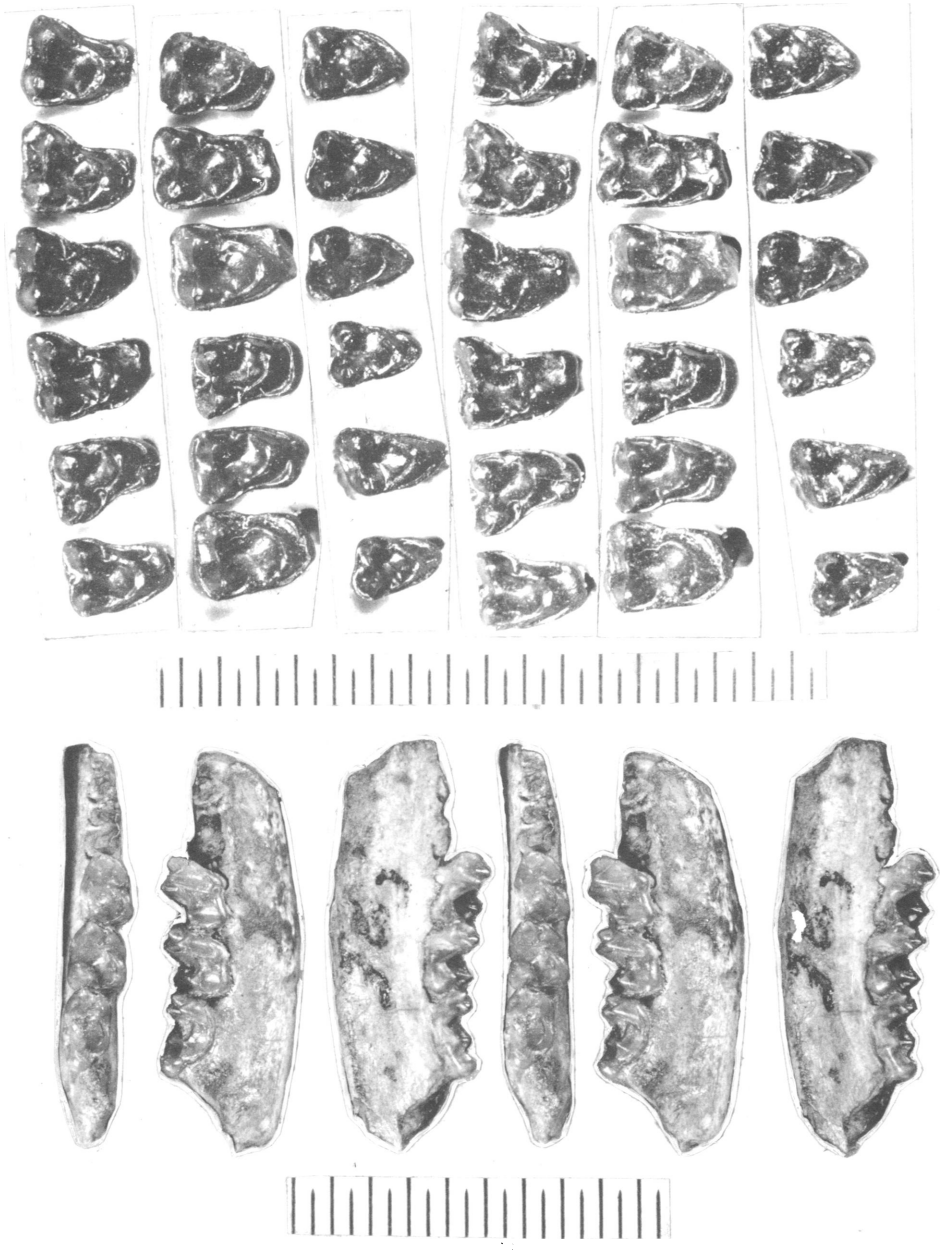


FIG. 66. *Omomys* sp., CM 6388, Powder Wash, Green River beds, upper molars (above). *Omomys minutus*, AC 3365, type, Lysite beds, right M_{1-3} (below). Stereophotographs: above and below left occlusal, below center lateral, and below right lateral views. Subdivisions on scales represent 0.5 mm.

Dental Formula. Probably the same as for other *Omomys.*

Discussion. There has been no new specimen added to the meager hypodigm of this species since Loomis's naming of the taxon. As noted by Kelly and Wood (1954, p. 344), Simpson (1940,

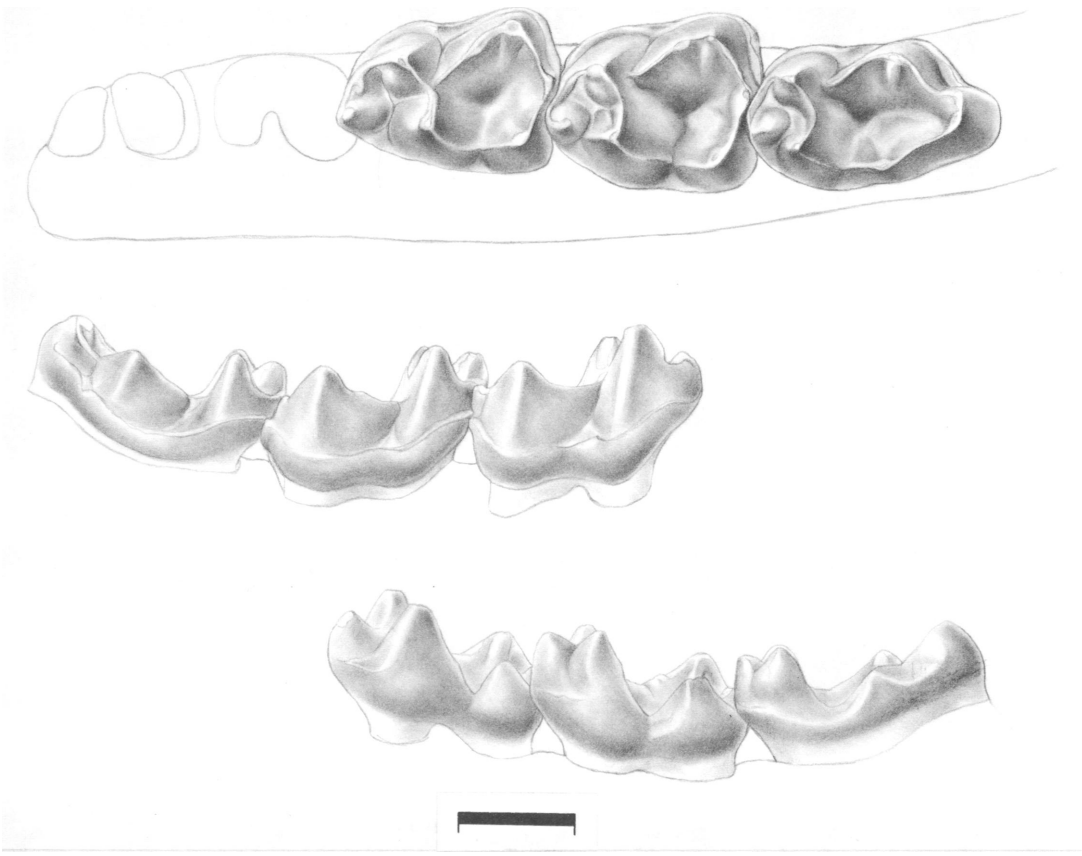


FIG. 67. *Omomys minutus*, right M_{1-3}, based on AC 3365, type, Wasatchian of Wyoming; occlusal (above), buccal (middle), and lingual (below) views. Scale represents 1 mm.

p. 189) questioned the assignment of this species to *Omomys*. This small species is very close to *Omomys lloydi* in size and there appear to be some morphological differences on the type which may warrant doubting the generic assignment to *Omomys*.

I believe that generic separation of *Omomys minutus* is at present not warranted. The teeth of *Omomys lloydi* and *Omomys minutus* are not of greatly different size, those of *Omomys lloydi* being slightly larger. The mandible of *Omomys minutus*, however, is distinctly shallower than that of specimens of *Omomys lloydi*. There is also a strong hint of relatively higher trigonid cusps in *Omomys minutus* and a more lingual paraconid, especially on M_2, than in either *O. carteri* or *O. lloydi*. These noted differences, on the other hand, should not be taken as necessarily diagnostic differences of generic rank. Better samples of this species will decide its eventual generic allocation.

Measurements in millimeters of the holotype are as follows: LM_2, 1.75; PWM_2, 1.50; AWM_2, 1.37; LM_3, 2.05; PWM_3, 1.26; AWM_3, 1.24.

CHUMASHIUS STOCK, 1933

Chumashius Stock, 1933, p. 954.

Type Species. Chumashius balchi Stock, 1933.

Included Species. Type species only.

Geographical and Temporal Distribution. Duchesnean (latest Eocene) of California.

Generic Diagnosis. Omomyines with relatively large canines and small incisors, low-crowned

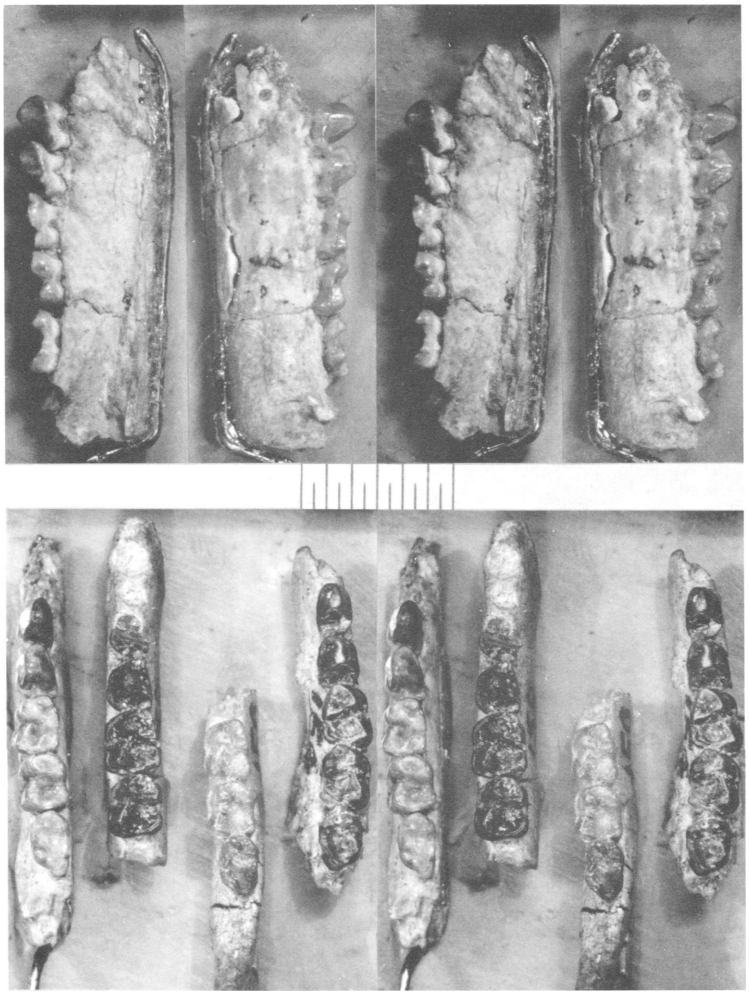
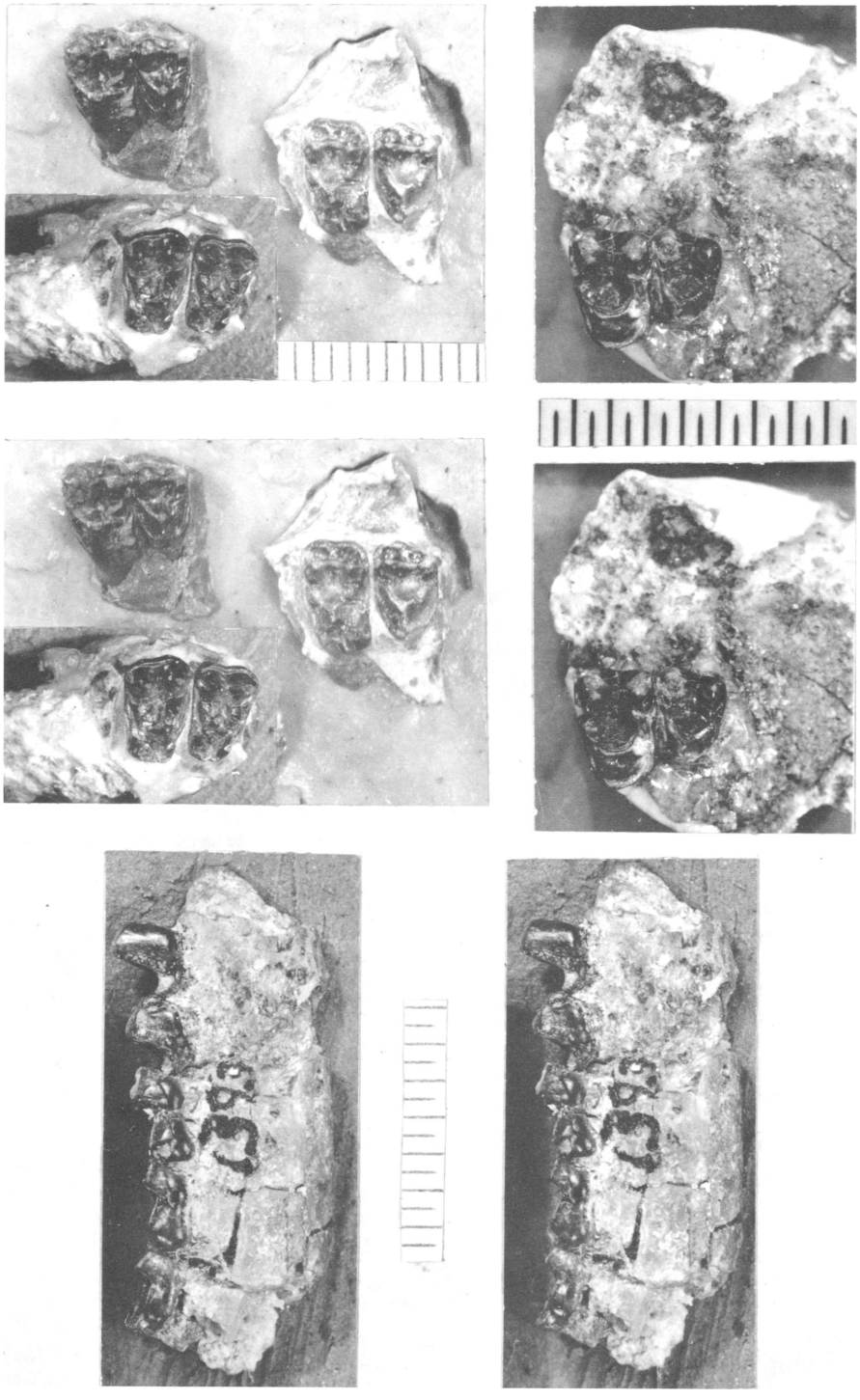


FIG. 68. *Chumashius balchi*, LACM 1391, type, left P_3-M_3 (above and extreme left below); LACM 1390, left P_3-M_2 (below center left); LACM 1392, left M_{1-3} (below center right); and LACM 1393, right P_3-M_3 (below extreme right); all from Sespe beds. Stereophotographs: above left medial, above right lateral, and below occlusal views. Subdivisions on scales represent 0.5 mm.

FIG. 69. *Chumashius balchi*, LACM 1394, left M^{2-3} (above right); LACM 1394, right P_3-M_3 (below); both Pearson Ranch, Sespe beds. *Dyseolemur pacificus*, LACM 5191, left M^{2-3} (above left); LACM 1528, left M^{2-3} (above center); both Tapo Ranch, Sespe beds. *Washakius woodringi*, LACM 2233, type, white sandstones associated with Poway conglomerate, right M^{1-2} (middle left). Stereophotographs: below lateral, all other occlusal views. Subdivisions on scales represent 0.5 mm.



molars, no apparent hypocone but lingually continuous pre- and post-cingula, and an M^3 distinctly less wide than M^2. The genus differs from *Omomys* in lacking the distinct pericone and hypocone of the latter, in having relatively less tall third and fourth premolars, and judged by the size of the alveoli, in having a relatively larger canine.

Discussion. When describing *Chumashius*, Stock (1933) clearly recognized that the closest ties of this genus were with *Omomys*. This view has been strengthened by Gazin (1958) and further supported on Chart 1 of Russell, Louis, and Savage (1967) who derived *Chumashius* directly from *Omomys*.

Chumashius is very similar to *Omomys* and this similarity appears to be a derived gestalt that these two genera share from a common ancestor. Yet, *Omomys* shows a number of more derived character states beyond such shared derived features as the heavy lingual cingulum and the lack of protocone-fold. Therefore, derivation of *Chumashius* from *Omomys* is much less likely than the reverse. *Omomys* was probably derived from a species which might be meaningfully referred to as *Chumashius*, although this ancestral species probably had relatively larger third molars than *Chumashius balchi*.

Adaptations. The trigonids are long mesiodistally and the paraconids are low, but distinct on M_1 and M_2. Correlated with the presence of distinct paraconids is the absence of a hypocone. The paraconid is well developed on P_4 with a long paracristid, and P_3 and P_4 are long mesiodistally. The teeth are flat, with relatively smooth enamel and the cingula are very well developed. The canines were not small or reduced but of fair size and the incisors were not relatively very large.

The long, shallow, straight (i.e., uncurved at the symphyseal region) horizontal ramus indicates no excessive transverse stressing of the mandible. The angle is not enlarged and therefore the specialization to increase the force of the internal pterygoids was not developed. Similarly, the shallow masseteric fossa signals the relative unimportance of the masseteric musculature. I can determine very little from the dental mechanism of this poorly known sample. The teeth, particularly the upper ones, show a great similarity to those of callithricids. Whether this is a synapomorphy or convergence does not detract from the suggestion that the dentition appears perhaps better suited for an insectivorous rather than a herbivorous diet.

Chumashius balchi Stock, 1933
Figures 68-71; Table 16

Chumashius balchi Stock, 1933, p. 954.

Type. LACM 1391, left mandible fragment with P_3-M_3; collected from Eocene Sespe beds, north of Simi Valley, CIT Vert. Paleo. loc. 150, Ventura County, California.

Hypodigm. The type and LACM 1390 and 1392, from the type locality; 1394 collected from Pearson Ranch locality.

Geographical and Temporal Distribution. Same as for genus.

Specific Diagnosis. Only known species of the genus.

Dental Formula. $I\frac{1,2}{1,2}; C\frac{1}{1}; P\frac{2,3,4}{2,3,4}; M\frac{1,2,3}{1,2,3}$.

Discussion. The angle on the reconstructed mandible of *Chumashius balchi* was taken from a photograph of LACM 1392 published by Stock (1933, pl. 1). The mandibular angle was not mentioned subsequently by students studying this specimen. As Gazin did not mention the angle on this specimen in 1958 it was presumably broken prior to his examination. Although some of Stock's comparisons may not be very significant today, his description of the sample is very thorough.

SUBTRIBE MYTONIINA ROBINSON, 1968

Type Genus. Mytonius Robinson, 1968 (considered a junior synonym of *Ourayia*).

Included Genera. Ourayia and *Macrotarsius*.

Subtribe Diagnosis. Omomyinines with robust, transversely narrowed, rugose molars. Anterior incisors, when known, are spatulate and rounded on their apex, and canines are relatively small.

Discussion. The genera included in this subtribe are the largest among the Omomyinae. This is perhaps significant in regard to their general adaptations because other known omomyids, as a rule, are small *Callithrix*- and *Tarsius*-sized ani-

TABLE 16
Numerical Data for Specimens of *Chumashius balchi* from Sespe Beds at the Pearson Ranch Localities

	LACM CIT 1390	LACM CIT 1392	LACM CIT 1393	LACM CIT 1394	*N*	OR	M
P_3							
L	–	–	2.30	–	1	–	–
PW	–	–	1.50	–	1	–	–
P_4							
L	2.30	–	2.38	–	2	2.30-2.38	2.34
PW	1.75	–	1.76	–	2	1.75-1.76	1.75
M_1							
L	2.54	2.45	–	–	2	2.45-2.54	2.49
PW	2.20	1.86	–	–	2	1.86-2.20	2.03
AW	2.10	1.76	–	–	2	1.76-2.10	1.98
M_2							
L	2.38	2.24	–	–	2	2.24-2.38	2.31
PW	2.12	1.88	–	–	2	1.88-2.12	2.00
AW	2.04	1.77	–	–	2	1.77-2.04	1.95
M_3							
L	–	2.56	–	–	1	–	–
PW	–	1.50	–	–	1	–	–
AW	–	1.56	–	–	1	–	–
M^2							
L	–	–	–	2.25	1	–	–
W	–	–	–	3.28	1	–	–
M^3							
L	–	–	–	1.94	1	–	–
W	–	–	–	2.52	1	–	–

mals. The dental adaptations, along with the hint of correlated size increase indicate perhaps enhanced adaptations to some form of phytophagy.

OURAYIA GAZIN, 1958

Microsyops: Osborn, 1895, p. 77.
?"*Microsyops*": Osborn, 1902, p. 202.
Omomys: Wortman, 1904, p. 134.
Ourayia Gazin, 1958, p. 70.
Hemiacodon: Robinson, 1968, p. 310.
Mytonius Robinson, 1968, p. 321.

Type Species. Ourayia uintensis (Osborn, 1895).

Included Species: Only known species of genus (see below).

Geographical and Temporal Distribution. Uintan (late Eocene) of Utah.

Generic Diagnosis. Omomyines with furrowed enamel, nearly squared molars, small hypocones and smaller pericones, and moderately large, spoon-shaped incisors. *Ourayia* differs from both *Omomys* and *Chumashius* in lacking the extensive lingual cingula, in having the crenulated enamel on the cheek teeth, and possessing relatively smaller third and fourth premolars. Differences from *Hemiacodon* are the distinctly less modified talonid, the relatively smaller hypocone, and the relatively smaller third and fourth premolars. *Ourayia* differs from *Macrotarsius* in having, judged from the alveoli, relatively larger canines and incisors and in having a symphysis both less extensive and more horizontally inclined. *Ourayia* lacks the derived cutting edge between the metaconid and entoconid, so characteristic of *Macrotarsius*.

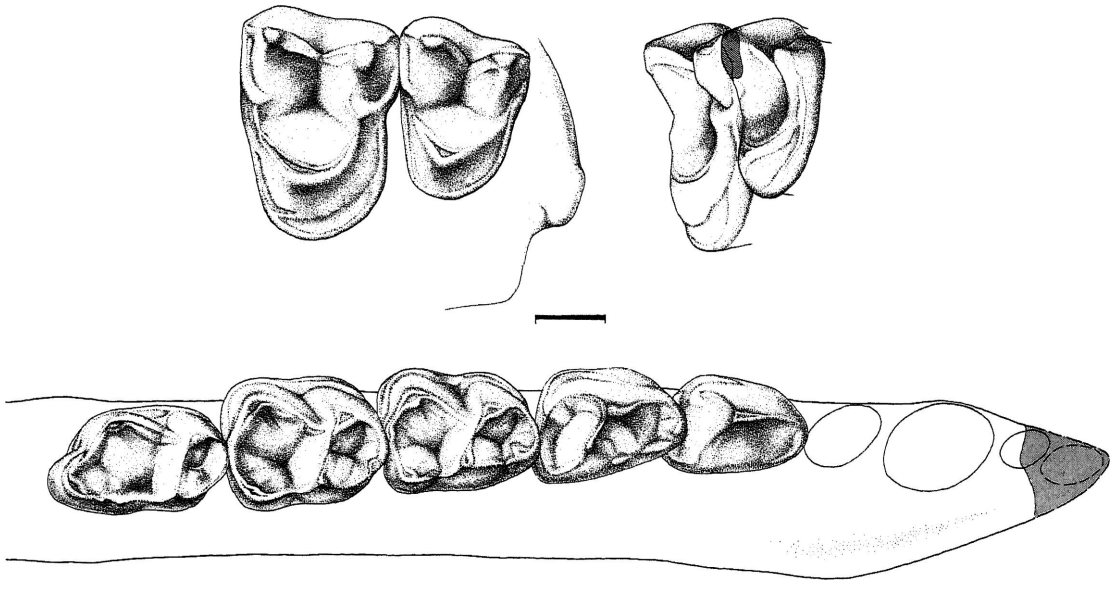


FIG. 70. *Chumashius balchi*, left M^{2-3} (above), based on LACM 1394 and left P_3-M_3 (below), based on LACM 1390, 1391, type, 1392, and 1393, both Uintan of California; occlusal (above left and below) and distal (above right) views. Reconstruction shown by uniform stippling and broken lines. Scale represents 1 mm.

Discussion. It was Wortman (1903, p. 134) who first recognized the family relationship of the generotype when he allocated it to *Omomys*. When describing the new genus *Ourayia* Gazin (1958, pp. 70-72) thoroughly compared the type species to *Hemiacodon* and considered it closest to the latter. This was misinterpreted by Simons (1961a, p. 3), who stated, "Gazin (1958) noted that this genus is close to later Eocene omomyids such as *Washakius*, *Hemiacodon* and *Stockia*." Gazin made no mention of *Washakius*, refuted his own earlier suggestion that *Stockia* is close to *Ourayia*, and decisively stated his belief on the closeness of *Ourayia* to *Hemiacodon*. Simons (1961a, p. 5) later specifically stated that *Ourayia* "may have been directly derived from *Hemiacodon*," a suggestion endorsed by Russell, Louis, and Savage (1967, p. 14).

Robinson (1968, p. 320), the last worker who dealt with the genus, chose to retain it as a valid taxon, trimming the hypodigm of the type species to be represented only by the holotype and AMNH 1900. He has briefly discussed the taxonomy of *Ourayia* and has taken two specimens, PU 11236 and 16431, both from Uinta B beds although from different localities, and erected a new species of *Hemiacodon*, *H. jepseni*. These specimens were previously referred to *Ourayia uintensis* by Simons (1961a), an allocation I support. Robinson has also taken a specimen, YPM 15266 from Uinta C beds (fig. 72), previously referred to *Ourayia*, and erected "*Mytonius hopsoni*," a new species, new genus, and a subfamily of Omomyidae based on the latter. I consider this action extreme. On the basis of minor differences of YPM 15266 and CM 12309, the latter an isolated M_2, the entire hypodigm of this species might be considered specifically distinct from the older *Ourayia uintensis*, but because even the specific distinction is questionable, generic or subfamily ranking of this poor sample is unacceptable.

Singularly inaccurate illustrations of *Ourayia uintensis* have been published by Simons (1972, p. 156), alongside those of *Ptilocercus lowii*, which was referred to as a generalized mammal. Several diastemata are shown in the dentition of the Eocene omomyid, which, in my opinion, are

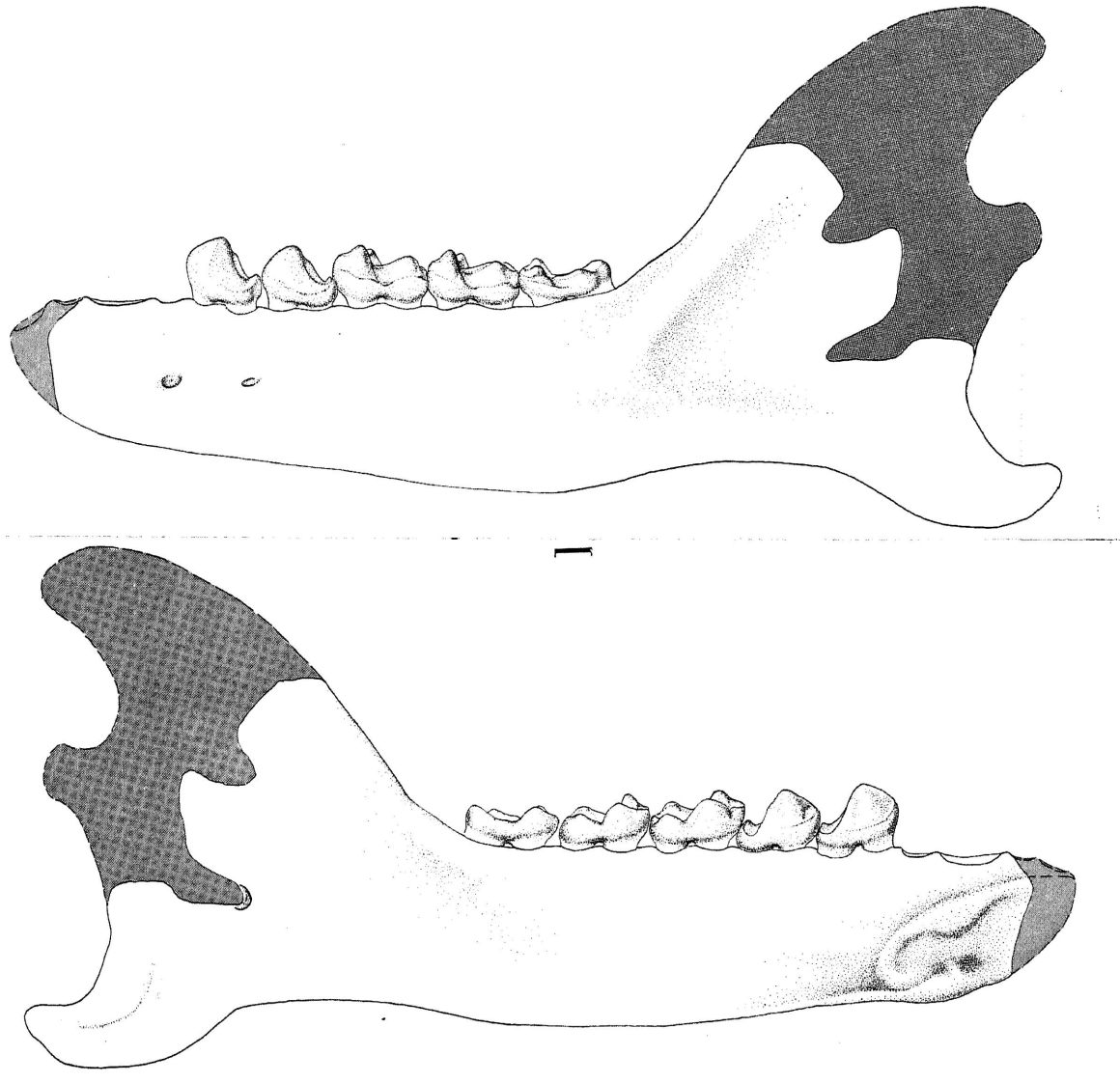


FIG. 71. *Chumashius balchi*, left mandible with P_3-M_3, based on LACM 1390, 1391, type, 1392, 1393, and Stock's original description and figures, Uintan of California; lateral (above) and medial (below) views, respectively. Reconstruction shown by uniform stippling and broken lines. Scale represents 1 mm.

artifacts of crushing. Both upper and lower central incisors are shown to be widely separated, an interpretation negated by wear. Depictions of the crown patterns of the teeth bear only vague resemblance to the specimens (see figs. 72-76 of this paper).

I find derivation of *Ourayia* from *Hemiacodon* highly unlikely. The large, cuspate hypocone and the unusual conformation of the large and relatively very broad talonid basin of the Bridger genus are derived features not possessed by *Ourayia*. Absence of a protocone-fold is a specializa-

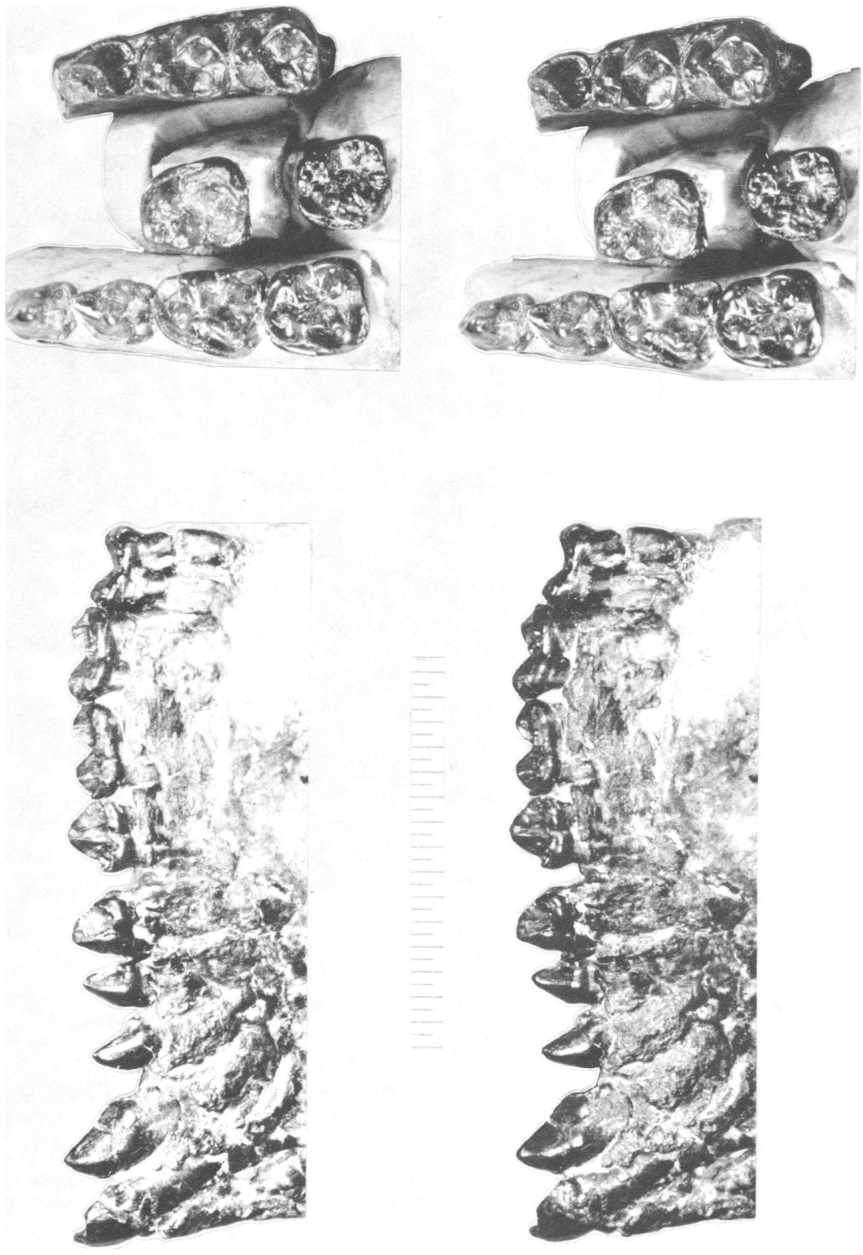


FIG. 72. *Ourayia uintensis*, AMNH 1899, type, right P_4-M_2 (top); AMNH 1900, left M_2 (second row right); AMNH 12309, right M_1 (second row left); YPM 15266, type of "*Mytonius hopsoni*," right P_3-M_2 (third row); PU 16431, type of "*Hemiacodon jepseni*," right I^1-M^3 (bottom); all from Uinta beds. Stereophotographs: above occlusal, below lateral views. Subdivisions on scale represent 0.5 mm.

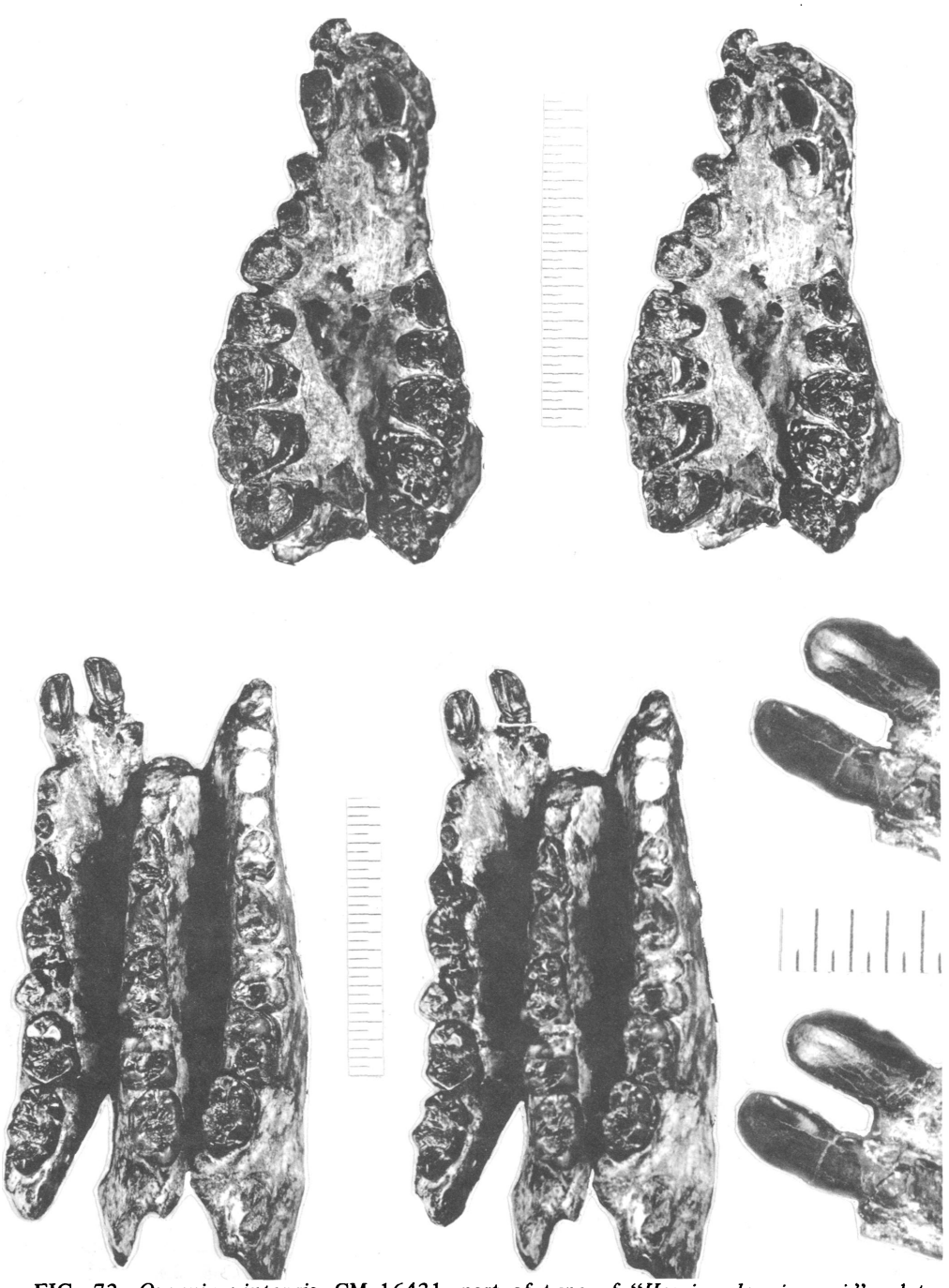


FIG. 73. *Ourayia uintensis*, CM 16431, part of type of "*Hemiacodon jepseni*," palate, lower jaw with central incisors, and P_3-M_3 (above, below right, and below left extreme); CM 11236, left mandible with P_3-M_3 and right mandible with broken P_3, P_4 and broken M_1, M_{2-3} (below left center and below left extreme right); all from Uinta beds. Stereophotographs: below right buccal, all others occlusal views. Subdivisions on scales represent 0.5 mm.

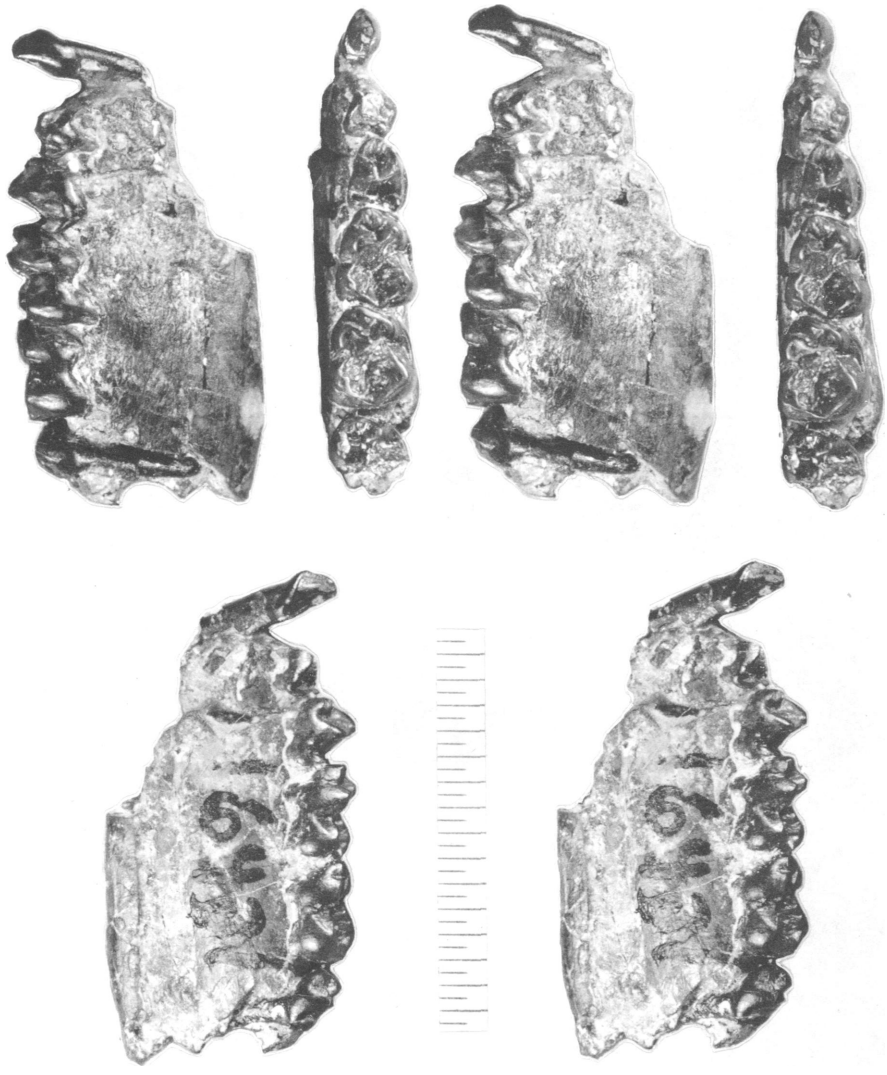


FIG. 74. *Ourayia uintensis*, PU 16431, part of type of "*Hemiacodon jepseni*," Uinta beds, right P_2-M_3. Stereophotographs: above left lateral, above right occlusal, below medial views. Subdivisions on scale represent 0.5 mm.

tion shared with *Omomys* and *Chumashius*, but the crenulated enamel of the crown surfaces is not necessarily a shared derived character with *Hemiacodon*. In light of the molar patterns it is likely that this latter feature is a specialization acquired independently from *Hemiacodon*. I consider derivation of *Ourayia* from *Omomys* or a genus near it more probable than an origin from *Hemiacodon*.

Adaptations. This genus is one of those few omomyids of which we have nearly the entire dentition preserved. By and large, the dentition is a "molar and incisor" dentition, inasmuch as the fourth and third premolars are distinctly smaller than the molars and the canine, at least the upper one, appears reduced.

The cheek teeth in general are characterized by crenulated enamel and particularly extensive

buccal cingula on P^3-M^3. Incipient mesostyles are present on the upper molars which have mesiodistally broad protocones but lack a protocone fold. Very small hypocones and tiny pericones are present on the first two upper molars. The lower molars have greatly expanded talonids, fairly tight talonid notches, and an extensive hypoconulid lobe on the third molar. Although the trigonids are mesiodistally wide, they are low and in general the cheek teeth are low-crowned.

As far as I can judge, the teeth formed a continuous, tightly packed battery that extended across the midline of the skull. The low, but mesiodistally extensive, crowns of the lower central incisor have a broad distal base from which the spoon-shaped continuous apical crest of this tooth emanates. The somewhat flat but apically rounded upper incisors are mesiodistally extensive. The two lower incisors and the lower canines apparently worked against the individually relatively larger first and second pairs of incisors, an arrangement one encounters in *Callicebus*, for example. The known mandibles are relatively robust, the symphysis clearly unfused, and the arrangement of the lower tooth row is somewhat long-limbed U-shaped rather than V-shaped.

The combined evidence suggests to me that *Ourayia uintensis* was primarily phytophagous, probably mainly frugivorous-omnivorous, with of course a probably significant portion of its diet coming from insect prey. The conformation of the molars, the smallness of the canines, and the morphology of the incisors suggest, however, no specializations for insectivory but rather for frugivory.

Ourayia uintensis (Osborn, 1895)
Figures 72-76; Table 17

Microsyops uintensis Osborn, 1895, p. 77.
?"*Microsyops*" *uintensis* Osborn, 1902, p. 202.
Omomys uintensis Wortman, 1904, p. 134.
Ourayia uintensis (Osborn, 1895) Gazin, 1958, p. 72.
Hemiacodon jepseni Robinson, 1968, p. 310.
Mytonius hopsoni Robinson, 1968, p. 321.

Type. AMNH 1899, left mandible fragment with P_3-M_2; collected from Uinta B beds, upper Eocene, White River Pocket, Uinta Basin, Utah.

Hypodigm. The type, and AMNH 1900, ?Uinta B beds; PU 16431, collected from Uinta B beds, White River Pocket; PU 11236, collected from Uinta B equivalent beds at Kennedy's Hole.

Geographical and Temporal Distribution. Uintan (late Eocene) of Utah.

Specific Diagnosis. Probably the only known species of the genus.

Dental Formula. $I\frac{1,2}{1,2}$; $C\frac{1}{1}$; $P\frac{2,3,4}{2,3,4}$; $M\frac{1,2,3}{1,2,3}$.

Discussion. It was noted under the generic discussion that Robinson (1968, p. 321) described a new species, new genus, and a new subfamily, all this based on YPM 15266, right jaw fragment with P_4-M_2 and CM 12309, an M_2, both collected from Uinta C beds, Myton Pocket, Utah.

The Uintan late Eocene "*Mytonius hopsoni*," pending the recovery of larger samples from Uinta C beds, may well turn out to be *Ourayia uintensis* of the Uinta B beds. No significant characters appear to separate this species from the generotype of *Ourayia*. The discussion of Robinson (1968, p. 321) refers to variation which may well have occurred within populations of *Ourayia uintensis*.

A specific distinction of the "*Mytonius hopsoni*" sample cannot be meaningfully maintained based on the known materials of the Uinta B and Uinta C samples. Were the Uinta C sample to improve and specific distinction from *Ourayia uintensis* become justifiable, generic separation from *Ourayia* will still be unlikely.

MACROTARSIUS CLARK, 1941

Macrotarsius Clark, 1941, p. 562.

Type Species. Macrotarsius montanus Clark, 1941.

Included Species. The type species and *Macrotarsius siegerti* Robinson, 1968.

Geographical and Temporal Distribution. Uintan to Chadronian (late Eocene to early Oligocene) of Wyoming and Montana.

Generic Diagnosis. Omomyines with relatively large molars, small premolars, and very small canines. Known materials of *Macrotarsius* differ from all other genera of omomyines in having the trigonid notch elevated to a widely open, shallow V-shaped crest between the metaconid and entoconid, and in having small cuspules, analogues of the metastylid of *Shoshonius* and *Washakius*, on a crest running basally and distally from the apical half of the metaconid.

TABLE 17
Numerical Data for Specimens of *Ourayia uintensis* from Uinta B Beds

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
I^2								
L	1	3.00	–	–	–	–	–	–
AW	1	1.55	–	–	–	–	–	–
L/AW	1	1.94	–	–	–	–	–	–
C								
L	1	2.16	–	–	–	–	–	–
AW	1	1.35	–	–	–	–	–	–
L/AW	1	1.60	–	–	–	–	–	–
P^2								
L	1	2.14	–	–	–	–	–	–
AW	1	1.35	–	–	–	–	–	–
L/AW	1	1.59	–	–	–	–	–	–
P^3								
L	1	3.15	–	–	–	–	–	–
AW	1	2.90	–	–	–	–	–	–
L/AW	1	1.09	–	–	–	–	–	–
P^4								
L	1	2.94	–	–	–	–	–	–
AW	1	3.70	–	–	–	–	–	–
L/AW	1	0.79	–	–	–	–	–	–
M^1								
L	1	3.80	–	–	–	–	–	–
AW	1	4.72	–	–	–	–	–	–
L/AW	1	0.81	–	–	–	–	–	–
M^2								
L	1	4.00	–	–	–	–	–	–
AW	1	5.08	–	–	–	–	–	–
L/AW	1	0.79	–	–	–	–	–	–
M^3								
L	1	3.55	–	–	–	–	–	–
AW	1	4.60	–	–	–	–	–	–
L/AW	1	0.77	–	–	–	–	–	–
I_1								
L	1	2.52	–	–	–	–	–	–
PW	1	1.90	–	–	–	–	–	–
L/PW	1	1.33	–	–	–	–	–	–
P_3								
L	3	2.90-3.40	–	3.100±0.153	0.265±0.108	9.246±3.775	–	–
PW	3	2.20-2.25	0.655	2.233±0.017	0.029±0.012	1.400±0.572	–	–
L/PW	3	1.32-1.51	–	1.388±0.062	0.107±0.044	8.376±3.420	–	–
P_4								
L	4	2.95-3.55	–	3.245±0.157	0.314±0.111	10.273±3.632	0.021	−5.629
PW	4	2.40-2.56	0.618	2.490±0.033	0.066±0.023	2.830±1.001	−0.877	1.934
L/PW	4	1.18-1.42	–	1.302±0.054	0.108±0.038	8.787±3.107	−0.086	−2.757
M_1								
L	4	3.70-4.55	–	4.087±0.176	0.352±0.124	9.152±3.236	0.612	1.330
PW	4	3.05-3.65	0.667	3.330±0.128	0.257±0.091	8.193±2.897	0.387	−0.616
AW	4	2.70-3.19	0.501	2.952±0.100	0.200±0.071	7.212±2.550	−0.223	1.478
L/PW	4	1.15-1.34	–	1.229±0.044	0.087±0.031	7.527±2.661	0.883	−0.467

TABLE 17—(*Continued*)

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
M_2								
L	6	3.64-4.40	–	4.007±0.108	0.264±0.076	6.872±1.984	0.266	0.012
PW	6	2.98-3.70	−0.422	3.443±0.118	0.290±0.084	8.771±2.532	−1.004	−0.611
AW	6	3.21-3.60	−0.022	3.333±0.060	0.147±0.043	4.608±1.330	1.463	1.877
L/PW	6	1.04-1.48	–	1.174±0.066	0.162±0.047	14.368±4.148	1.671	2.846
M_3								
L	2	4.55-5.22	–	–	–	–	–	–
PW	2	3.10	–	–	–	–	–	–
AW	2	2.91-3.10	–	–	–	–	–	–
L/PW	2	1.47-1.68	–	–	–	–	–	–

Discussion. In his phylogeny of North American Eocene and early Oligocene primates Gazin (1958) clearly included *Macrotarsius* in the Omomyidae. He derived it from unknown stocks of medial Eocene forms, although the unknown ancestry was in a position between *Washakius* and a *Utahia-Stockia* lineage.

Simons (1961a, p. 5) suggested the derivation of *Macrotarsius montanus* from *Ourayia* and Russell, Louis, and Savage (1967, p. 4), in discussing omomyine affinities, noted that *Macrotarsius*, "beyond a general resemblance to *Washakius* and *Hemiacodon*, cannot be said to be a direct descendant of the known Eocene forms." In describing a new species of *Macrotarsius*, Robinson (1968) clearly implied that a phyletic continuum, *Hemiacodon-Ourayia-Macrotarsius*, occurred, even though he did not recognize the generic distinction of *Ourayia* from *Hemiacodon*.

Macrotarsius is clearly more derived in its known morphology than *Ourayia*. Because of a geographical proximity, a near temporal sequence, and a categorization of *Ourayia* as more primitive and *Macrotarsius* as more derived, I tentatively suggest some form of *Ourayia* to be ancestral to *Macrotarsius*. There are no clear-cut shared derived features to back this derivation, although the squared molars of the two genera may represent such a synapomorphy.

Adaptations. I can ascertain no differences other than size between the holotype of *M. montanus* and the sample of *M. siegerti*. Thus, all the remarks on the lower dentition pertain with equal weight to both samples.

Macrotarsius has a maximum of cheek tooth crests with relatively narrow bases. The trigonids are V-shaped, dominated by the relatively straight crests with very little apical relief. The external wall of the cristid obliqua, as that of the buccal portion of the postcristid, is hollowed out. Diagnostic crests run between the paraconid and metaconid and the latter and the entoconid. Buccal cingula are prominent and the anterior cingulid on the lower molars is particularly pronounced. To the long ectolophs and extensive protocone crests are added well-developed mesostyles, although the conules are not especially large.

The canine is relatively small and, judged from the incisor alveoli, the dentition anterior to it was not particularly enlarged.

The extensive crests on the large molars, which virtually lack rounded, bulbous cusps, and the unenlarged anterior teeth suggest to me folivory as a dietetic specialization rather than insectivory or frugivory. Considerably strengthening this inference is the convergent similarity of the molar gestalt of *Macrotarsius* to those of *Alouatta*, a confirmed folivore.

Macrotarsius montanus Clark, 1941
Figures 77, 78

Macrotarsius montanus Clark, 1941, p. 562.

Type. CM 9592, right mandible with C and P_3-M_3; collected from north face of range, 1½ miles southeast of Cold Springs, North Boulder Valley, Jefferson County, Montana.

Hypodigm. Type only.

Geographical and Temporal Distribution. Chadronian (early Oligocene) of Montana.

Specific Diagnosis. Larger than *M. siegerti.*

Dental Formula. $I\frac{1,2}{1,2}$; $C\frac{1}{1}$; $P\frac{2,3,4}{2,3,4}$; $M\frac{1,2,3}{1,2,3}$.

Discussion. The holotype, still the only hypodigm of this species, was briefly and well described by Clark (1941). The following represent measurements in millimeters of the holotype:

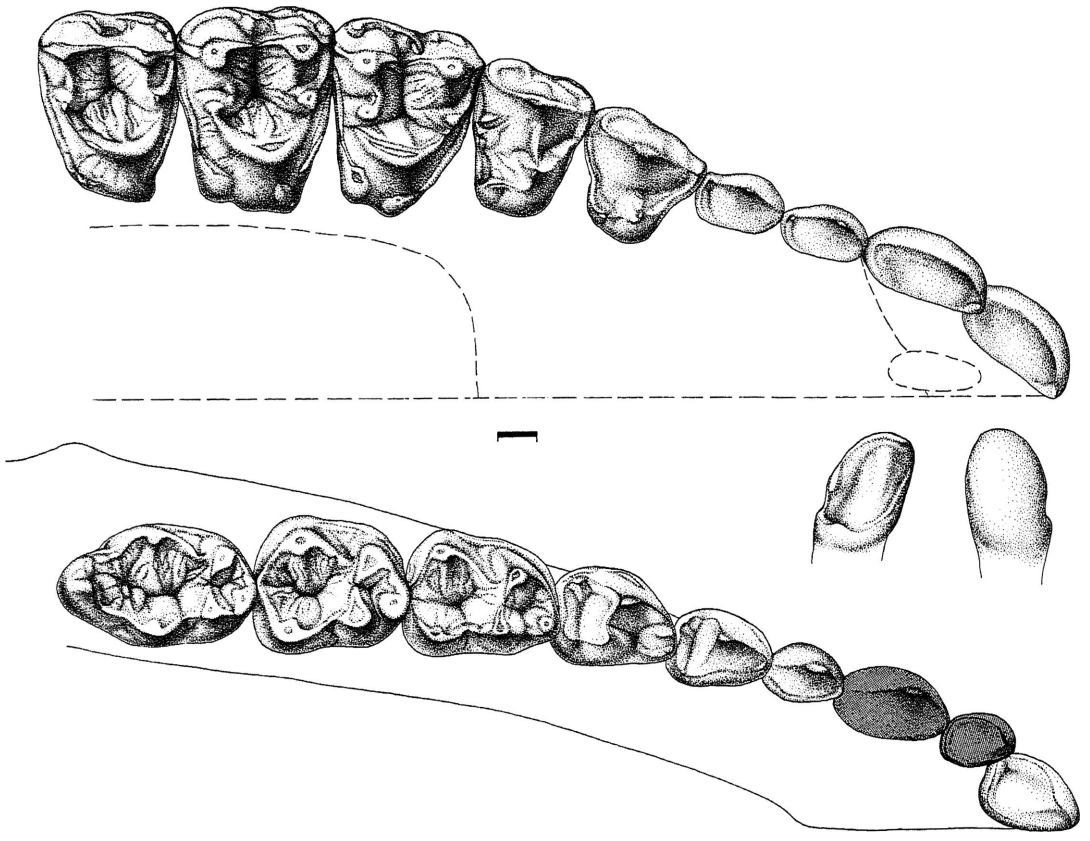


FIG. 75. *Ourayia uintensis*, upper right (above) and lower left (below) dentitions, based on PU 16431, type of "*Hemiacodon jepseni*," and PU 11236, Uintan of Utah; occlusal views. From left to right on the middle right are lingual and buccal views, respectively of the left I_1. Reconstruction shown by uniform stippling. Scale represents 1 mm.

LP_4, 3.32; PWP_4, 3.05; LM_1, 4.58; PWM_1, 3.95; AWM_1, 3.65; LM_2, 4.50; PWM_2, 3.89; AWM_2, 3.83; LM_3, 5.86; PWM_3, 3.70; AWM_3, 3.44.

Macrotarsius siegerti Robinson, 1968
Figures 79-81; Table 18

Macrotarsius siegerti Robinson, 1968, p. 312.

Type. CM 15122, right P_4; collected from loc. 5A of Carnegie Museum, Badwater Creek Area, Wyoming.

Hypodigm. The type and CM 14549, 14601, 15056, 15068, 15072, 15147, 15610, 15674, 15717, 18646, UCM 26009, 1-UCM 25276, all collected from various late Eocene Badwater Creek localities (5 front, 5 back, 5A, 6, Wood) of the Carnegie Museum, see Black and Dawson (1966).

Geographical and Temporal Distribution. Uintan (late Eocene) of Wyoming.

Specific Diagnosis. Smaller than the genero-type, *M. montanus*.

Dental Formula. Probably the same as for *M. montanus*.

Discussion. Contrary to Robinson's (1968, p. 314) statement that this species would be difficult to distinguish from "*Hemiacodon jepseni*," i.e., from *Ourayia uintensis*, on the basis of isolated lower molars, the crest on the molar talonids between the entoconid and metaconid is clearly diagnostic of this species and other *Macrotarsius*.

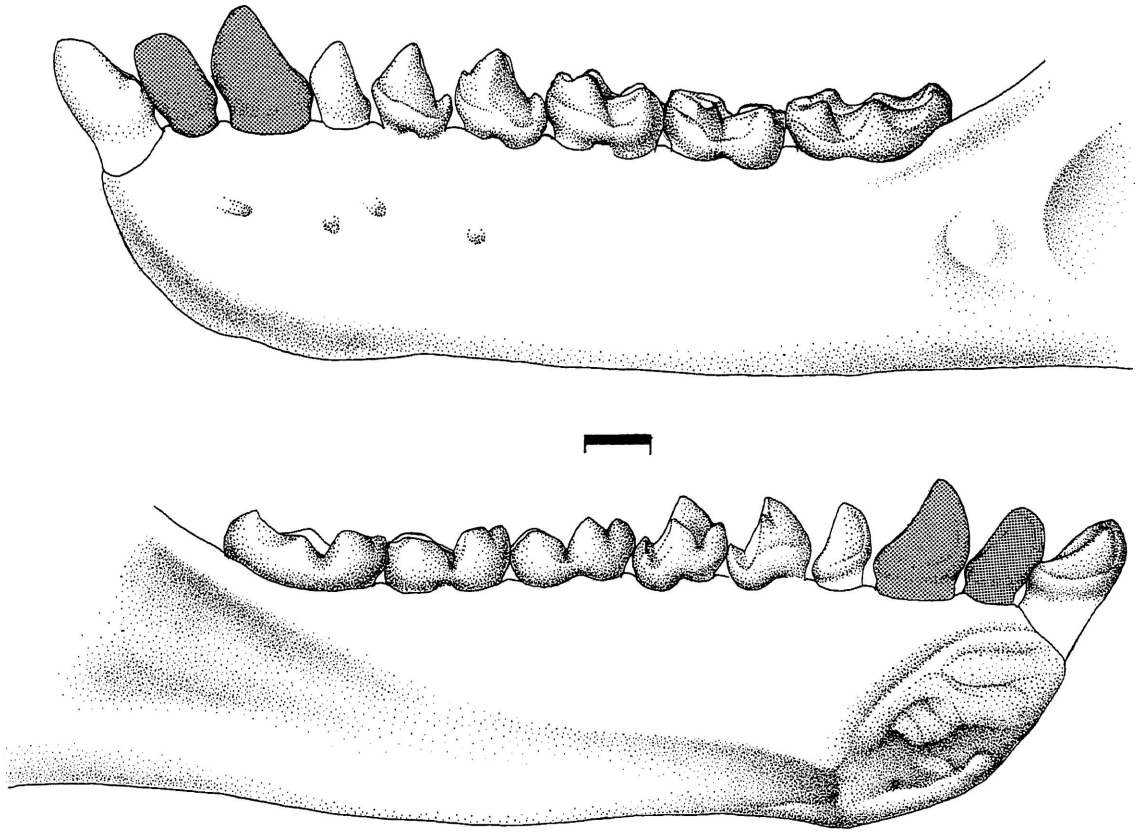


FIG. 76. *Ourayia uintensis*, based on PU 16431 and 11236, Uintan of Utah, left horizontal ramus with I_1-M_3; lateral (above) and medial (below) views. Reconstruction shown by uniform stippling and broken lines.

In addition to the statistics presented in table 18 of this work, the individual measurements of known *Macrotarsius siegerti* specimens may be found in Robinson (1968).

TRIBE WASHAKIINI, NEW

Type Genus. Washakius Leidy, 1873.

Included Taxa. Type genus and *Loveina* Simpson, 1940, *Shoshonius* Granger, 1910, *Dyseolemur* Stock, 1934, and *Hemiacodon* Marsh, 1872.

Tribe Diagnosis. Omomyines with both a protocone-fold and a moderately developed hypocone (except in *Loveina* and *Shoshonius*).

Discussion. Great widening of the talonids appears to be a primitive trait of this group. Although this feature reaches an extreme in *Hemiacodon* and the upper molars of that genus appear to be very similar to those of *Loveina*, allocation of the former to this tribe is not at all certain.

As noted below the metastylid is believed to be a shared derived character between *Shoshonius* and *Washakius.*

LOVEINA SIMPSON, 1940

Loveina Simpson, 1940, p. 188.
Tetonius: Seton, 1940, p. 41.

Type Species. Loveina zephyri Simpson, 1940.

Geographical and Temporal Distribution. Late Wasatchian (late early Eocene) of Wyoming and Colorado.

FIG. 77. *Macrotarsius montanus*, CM 9592, type, Chadronian of Montana, right C and P_3-M_3. Stereophotographs: above left lateral, above right occlusal, below medial views. Subdivisions on scale represent 0.5 mm.

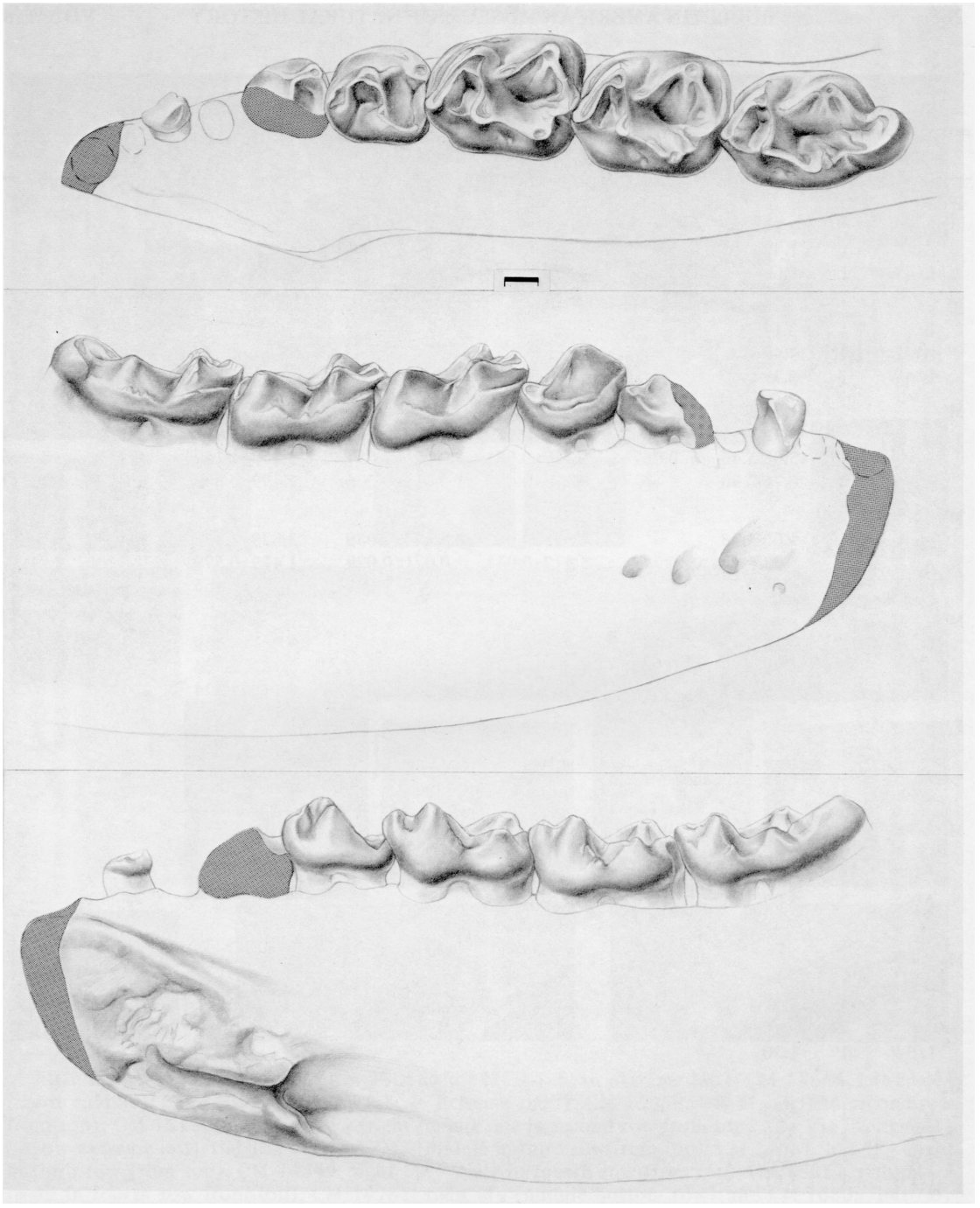


FIG. 78. *Macrotarsius montanus*, CM 9592, type, Chadronian of Montana, right horizontal ramus with C and P_3-M_3; occlusal (above), lateral (middle), and medial (below) views. Reconstructions shown by uniform stippling and by broken lines. Scale represents 1 mm.

TABLE 18
Numerical Data for Specimens of *Macrotarsius siegerti* from Various Badwater Localities

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P^2								
L	1	2.24	–	–	–	–	–	–
AW	1	1.40	–	–	–	–	–	–
L/AW	1	1.60	–	–	–	–	–	–
P^4								
L	1	3.14	–	–	–	–	–	–
AW	1	4.40	–	–	–	–	–	–
L/AW	1	0.71	–	–	–	–	–	–
M^1								
L	4	3.92-4.14	–	4.055±0.049	0.097±0.034	2.554±0.903	−1.210	1.034
AW	4	5.08-5.45	0.667	5.250±0.081	0.161±0.057	3.259±1.152	0.431	−1.196
L/AW	4	0.76-0.80	–	0.773±0.009	0.018±0.006	2.499±0.883	1.079	−0.097
M^2								
L	3	4.00-4.25	–	4.083±0.083	0.144±0.059	3.829±1.563	–	–
AW	3	5.34-5.48	0.773	5.417±0.041	0.071±0.029	1.419±0.579	–	–
L/AW	3	0.74-0.78	–	0.754±0.011	0.020±0.008	2.856±1.166	–	–
M^3								
L	3	3.11-3.80	–	3.437±0.200	0.346±0.141	10.921±4.459	–	–
AW	3	4.72-5.19	0.900	4.880±0.155	0.269±0.110	5.961±2.434	–	–
L/AW	3	0.66-0.73	–	0.703±0.023	0.040±0.016	6.182±2.524	–	–
P_4								
L	1	3.35	–	–	–	–	–	–
PW	1	2.96	–	–	–	–	–	–
L/PW	1	1.13	–	–	–	–	–	–
M_1								
L	2	3.99-4.44	–	–	–	–	–	–
PW	2	3.31-3.38	–	–	–	–	–	–
AW	2	3.00-3.15	–	–	–	–	–	–
L/PW	2	1.18-1.34	–	–	–	–	–	–
M_2								
L	1	4.31	–	–	–	–	–	–
PW	1	3.58	–	–	–	–	–	–
AW	1	3.46	–	–	–	–	–	–
L/PW	1	1.20	–	–	–	–	–	–
M_3								
L	1	4.98	–	–	–	–	–	–
PW	1	3.10	–	–	–	–	–	–
AW	1	3.10	–	–	–	–	–	–
L/PW	1	1.61	–	–	–	–	–	–

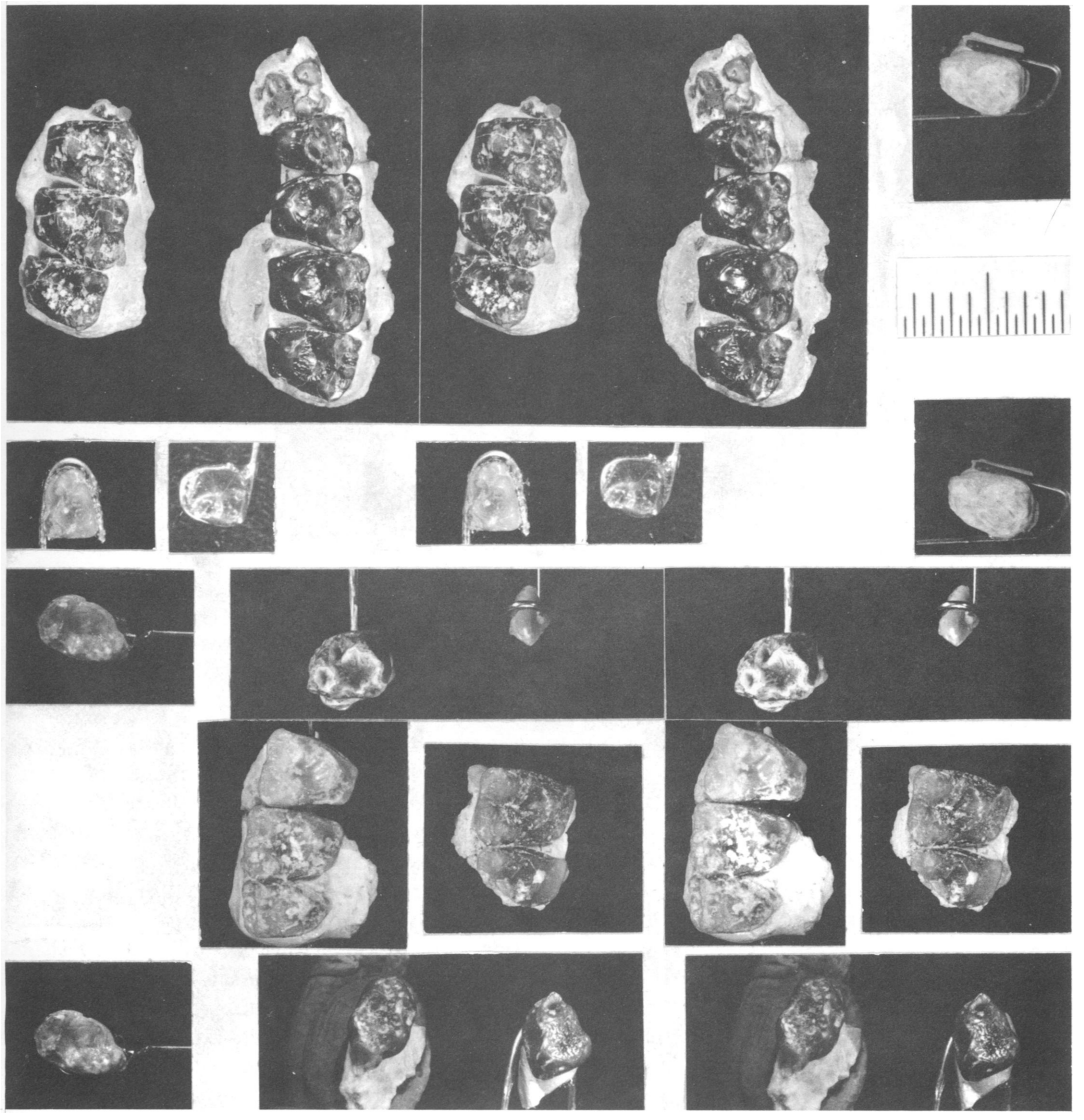


FIG. 79. *Macrotarsius siegerti*, CM 15056, left M^{1-3} (above extreme left); CM 18646, left P^4-M^3 (above middle); CM 16063, right M_1 (above extreme right); CM 15068, left M_1 (left in second row from top); CM 15122, type, right P_4 (right on left side in second row from top); CM 15674, right M_3 (below extreme left); CM 15147, right ?M_1 (middle in third row from top); CM 14551, left ?P^2 (right in third row from top); CM 14549, right M^{1-3} (left in fourth row from top); CM 15052, right M^{2-3} (right in fourth row from top); CM 19761, right M_3 (middle bottom row); and CM 16809, left ?M_1 (right bottom row). Stereophotographs: CM 14551 buccal, all others occlusal views. Subdivisions on scale represent 0.5 mm.

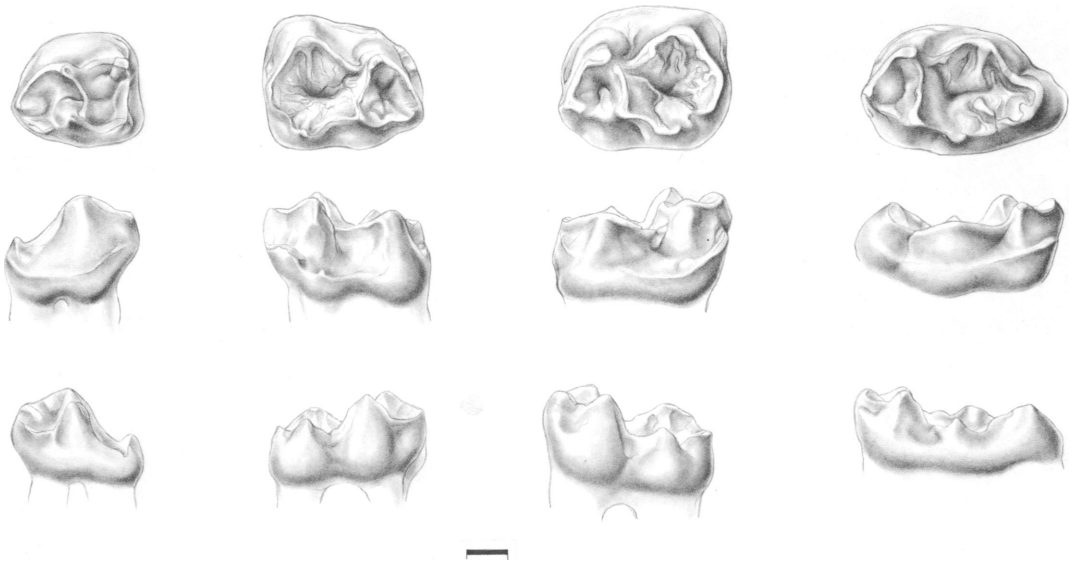


FIG. 80. *Macrotarsius siegerti*, left to right: CM 15122, type, right P_4; CM 16809, left M_1, CM 15147, right M_2; and CM 15647 and 19761, combined, right M_3; occlusal (above), buccal (middle), and lingual (below) views. Scale represents 1 mm.

Generic Diagnosis. Omomyines with protocone-fold, moderate canines, and small incisors. *Loveina* differs from its closest relatives, *Shoshonius* and *Washakius*, in lacking a metastylid. Unlike *Washakius*, *Loveina* lacks the double metaconule and the cuspate, distinct hypocone, and small pericone. Unlike *Shoshonius* it lacks a mesostyle.

Discussion. Simpson (1940, pp. 188-189), when describing this genus, pointed out that *Loveina*'s closest known relatives are probably *Washakius* and *Shoshonius*. Gazin (1958), who astutely suggested that MCZ 3495, a maxilla with four teeth (figs. 82 and 84), might be allocated to *Loveina zephryi* (p. 25), apparently agreed with Simpson's phyletic inferences. He showed *Loveina*, *Washakius*, and *Shoshonius* to be very near to a common ancestor for all three (Gazin, 1958, chart 1). In their interpretations of phyletic relationships Russell, Louis, and Savage (1967, fig. 14) refrained from any suggestion as to the closest ties of *Loveina* within the Omomyidae.

I strongly agree with Simpson (1940) and Gazin (1958) concerning the recency of affinities of *Loveina*. There are, however, a few features which perhaps allow some minor refinements in the details of the phyletics of these taxa. On the slope mesiolingual to the metacone there is a unique, tiny cuspule in MCZ 3495; on the homologous area in the upper teeth of *Shoshonius* one, two, or three similar wrinkles can be found. Sharing this character with *Shoshonius*, but not the metastylid and the mesostyle, indicates speciation prior to the acquisition of the latter characters. Sharing of the metastylid by *Shoshonius* and *Washakius* suggests separation of the ancestral species of these genera after *Loveina* became phyletically distinct from the common *Shoshonius-Washakius* stock.

Loveina is an extremely important omomyid. It is perhaps one of the most primitive of the known taxa of the subfamily in its molar and premolar morphology, and the anterior dentition, judged by the alveoli, does not appear to be particularly advanced.

Adaptations. The unique combination of adaptations of *Loveina* lie in the relatively small canines, small incisors, crenulated teeth, relatively very broad talonids, squared off first and second upper molars which do not have a hypocone, and the presence of distinguishable superior and inferior transverse tori.

The small size and all the molar features sug-

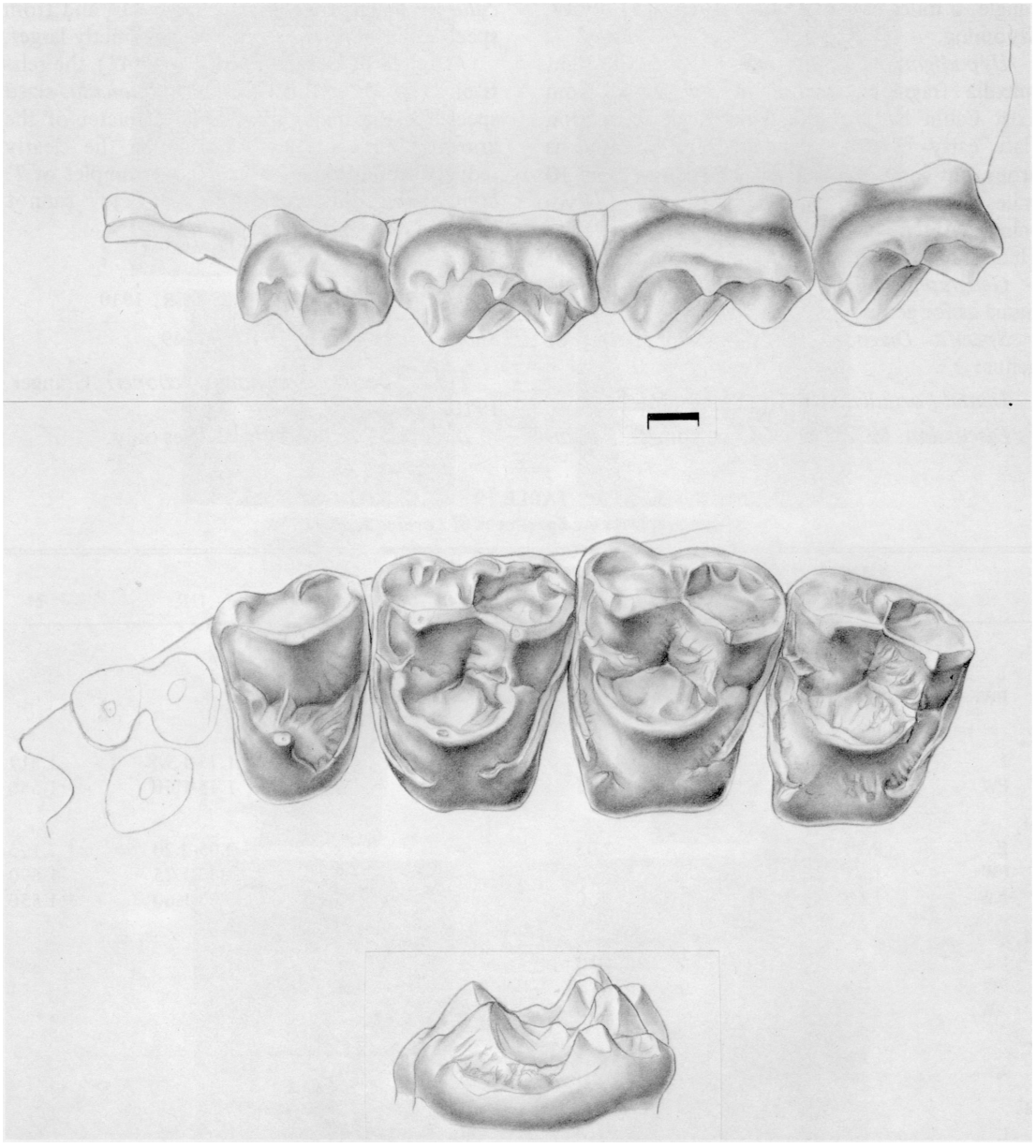


FIG. 81. *Macrotarsius siegerti*, CM 18646, Uintan of Wyoming, left P^4-M^3; buccal (above), occlusal (middle), and distal (below) views. Scale represents 1 mm.

gest a probably frugivorous-insectivorous gestalt of adaptations.

Loveina zephyri Simpson, 1940
Figures 82-84; Table 19

Loveina zephyri Simpson, July, 1940, p. 188.

Tetonius barbeyi Seton, August, 1940, p. 41.

Type. AMNH 32517 left jaw fragment with P_3-M_1 and alveoli of P_2, canine, and two incisors; collected from Wind River Formation, Lost Cabin beds near head of Badlands Gulch at the south end of Table Mountain, Kirwin Quad-

rangle, 6 miles east of Dubois, Fremont County, Wyoming.

Hypodigm. The type and MCZ 3495, right maxilla fragment with P^4-M^3, collected from Lost Cabin beds of the Wind River Formation (late early Eocene), same beds as the type is from, but some distance away (Muddy Creek, 10 miles north of Pavillion, Wind River Basin, Wyoming); AMNH 55219 and 17554 from lower Huerfano beds.

Geographical and Temporal Distribution. Same as for genus.

Specific Diagnosis. Only known species of genus.

Dental Formula. $I\frac{1,2}{1,2}; C\frac{1}{1}; P\frac{2,3,4}{2,3,4}; M\frac{1,2,3}{1,2,3}$.

Discussion. MCZ 3495 differs from *T. homunculus* in having a relatively larger M^3 and from species of *Anemorhysis* in being distinctly larger.

As noted by Seton (1940, pp. 41-42), the relatively large M^3 in this *Tetonius homunculus*-sized species is the major diagnostic character of the known sample of one. Considering the clearly reduced condition of M^3 in large samples of *T. homunculus*, the type of "*T. barbeyi*" cannot be referred to the former taxon.

SHOSHONIUS GRANGER, 1910

Shoshonius Granger, 1910, p. 249.

Type Species. Shoshonius cooperi Granger, 1910.

Included Species. Type species only.

TABLE 19
Numerical Data for Specimens of *Loveina zephyri*

	AMNH 32517	AMNH 55219	AMNH 17554	MCZ 3495	*N*	OR	M
P_3							
L	1.60	–	–	–	1	–	–
PW	1.40	–	–	–	1	–	–
P_4							
L	1.80	1.90	1.75	–	3	1.75-1.90	1.817
PW	1.60	1.60	1.45	–	3	1.45-1.60	1.550
M_1							
L	2.20	–	2.05	–	2	2.05-2.20	2.125
PW	1.75	–	1.63	–	2	1.63-1.75	1.690
AW	1.60	–	1.50	–	2	1.50-1.60	1.550
M_2							
L	–	–	2.10	–	1	–	–
PW	–	–	1.73	–	1	–	–
AW	–	–	1.60	–	1	–	–
P^4							
AW	–	–	–	2.65	1	–	–
M^1							
L	–	–	–	2.0	1	–	–
AW	–	–	–	2.9	1	–	–
M^2							
L	–	–	–	2.12	1	–	–
AW	–	–	–	3.3	1	–	–
M^3							
L	–	–	–	1.9	1	–	–
AW	–	–	–	2.84	1	–	–

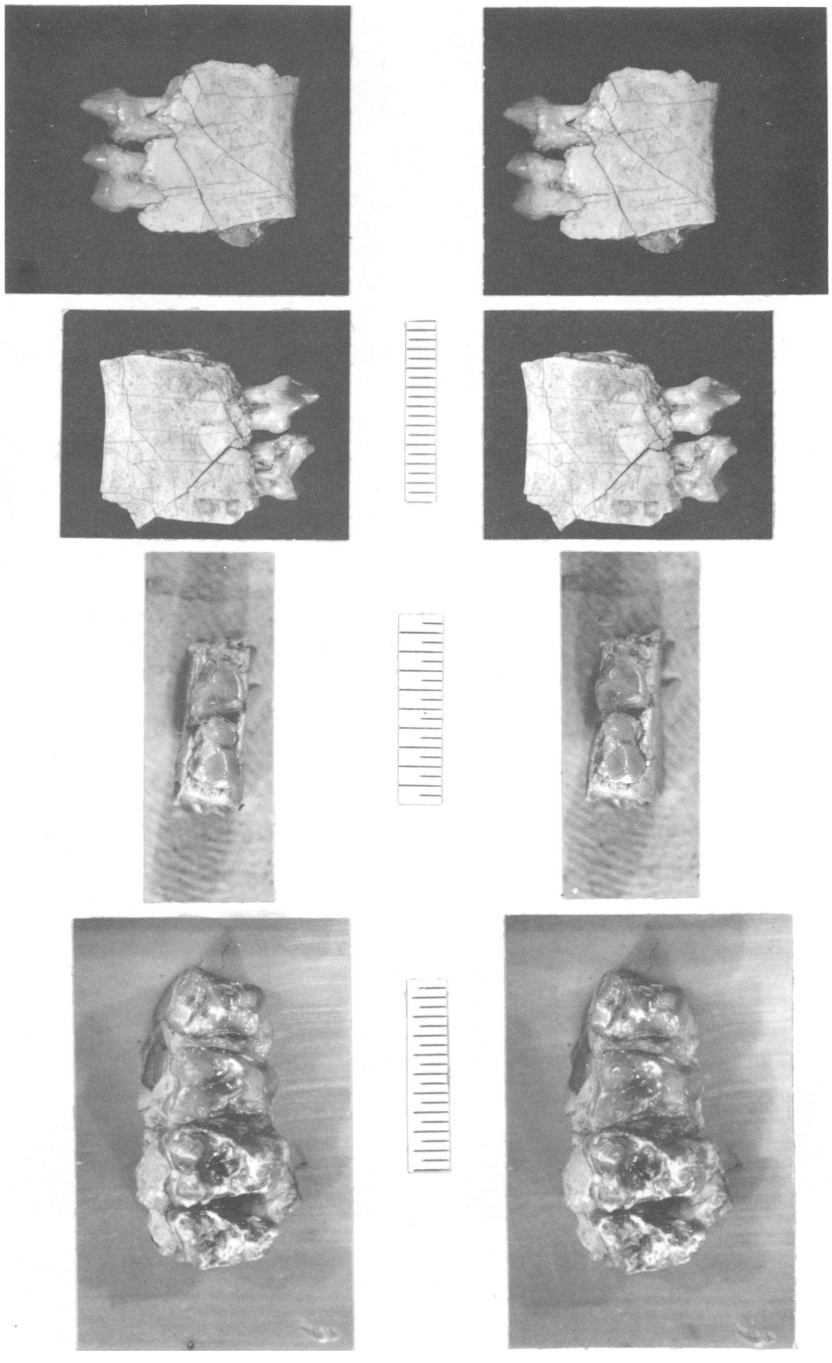


FIG. 82. *Macrotarsius*? sp., CM 10855, Chadronian, right P_4-M_1 (top three rows). *Loveina zephyri*, MCZ 3495, Lost Cabin beds, right P^4-M^3 (bottom). Stereophotographs: above lateral, second row medial, third row and bottom occlusal views. Subdivisions on scales represent 0.5 mm.

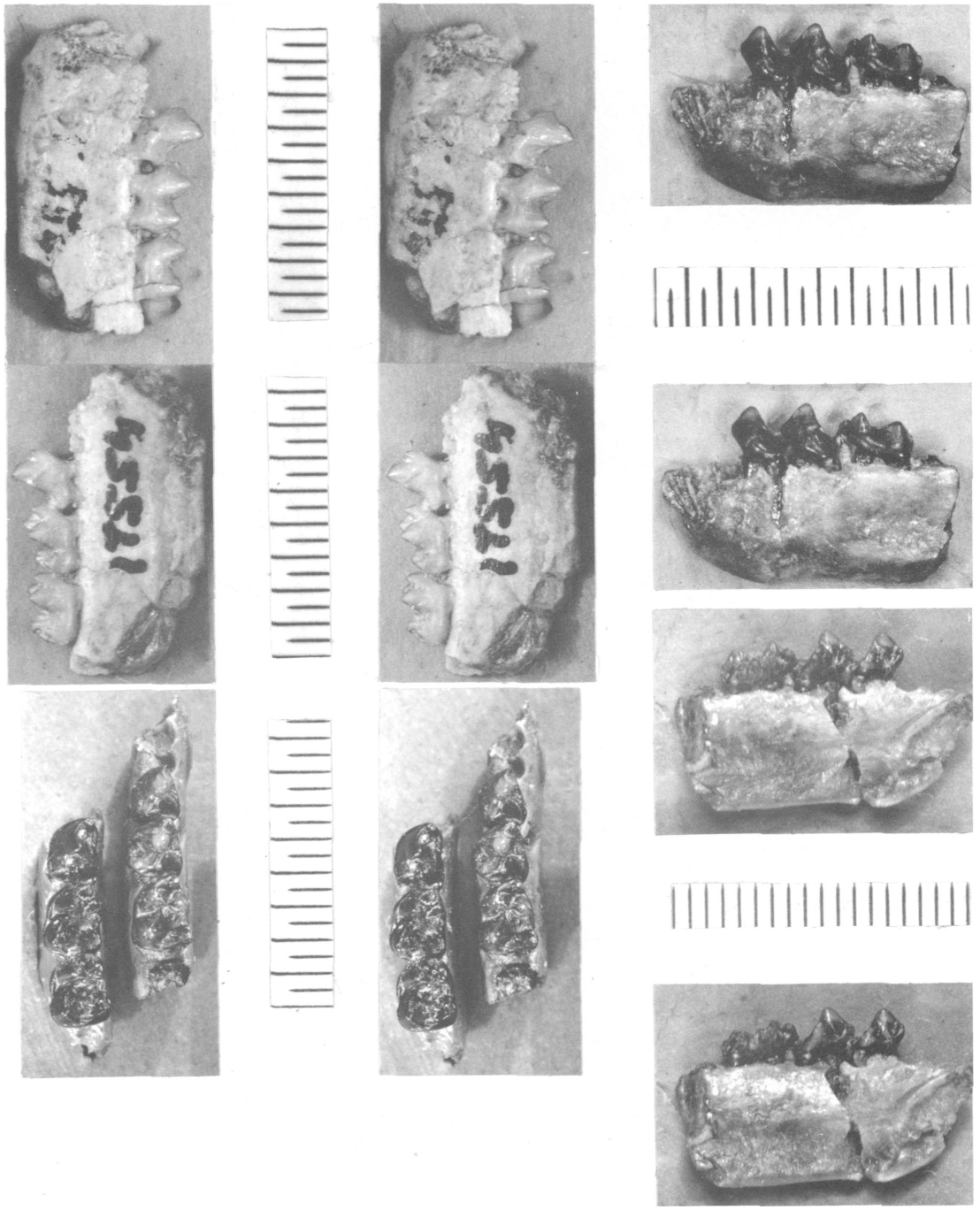


FIG. 83. *Loveina zephyri*, AMNH 32517, type, Lost Cabin beds, left P_3-M_1 (right and below center); AMNH 17554, loc. VI, Huerfano beds, left P_4-M_2 (above and middle left). *Omomys lloydi*, CM 6417, type, Powder Wash, Green River beds, left P_4-M_2 (below left). Stereophotographs: above lateral, middle and below right medial, and below left occlusal views. Subdivisions on scales represent 0.5 mm.

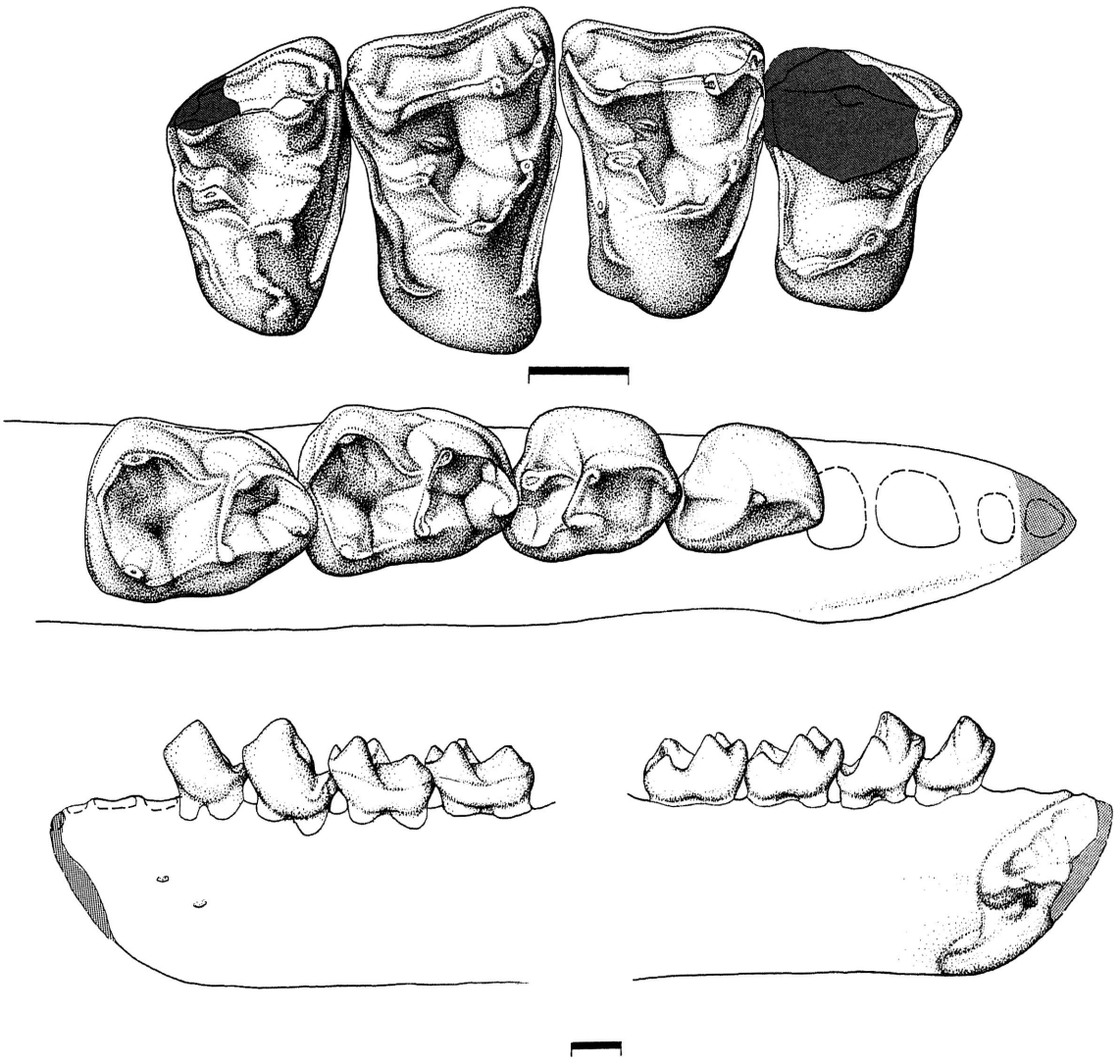


FIG. 84. *Loveina zephyri*, MCZ 3495, left P^4-M^3 (above), part of left mandible and P_3-M_2 based on AMNH 32517, type, and AMNH 17554, late Wasatchian of Wyoming and Colorado (middle and below left and right); above and middle occlusal, below lateral and medial views, respectively. Reconstruction shown by uniform stippling, hatching, and broken lines. Scales represent 1 mm.

Geographical and Temporal Distribution. Late Wasatchian, "Lost-cabinian" (late early Eocene) of Wyoming and Colorado.

Generic Diagnosis. Omomyids with protocone-fold, mesostyle, and metastylid. *Shoshonius* differs from *Loveina* in all the above specializations and from *Washakius* in having the well-developed mesostyle, a metacone on P^3 and P^4, and, unlike the latter, in lacking a cuspate hypocone.

Discussion. This genus has been seldom discussed, mainly because of the relative paucity of specimens. Gazin's (1958, chart 1) phylogeny shows *Shoshonius* and *Washakius* derived from a common ancestry, and Russell, Louis, and Savage (1967, p. 3) stated that *Shoshonius* is in general

similar to *Washakius*. The latter authors do not, however, show close phyletic derivation for the two, as for example they do on the same chart for *Ourayia* and *Hemiacodon*.

The nature of similarity between *Loveina* and *Shoshonius* has been discussed above in the treatment of the former genus. Evaluation of the resemblances suggests derivation of *Shoshonius* from an ancestor very much like *Loveina zephyri*.

When *Shoshonius* is compared with *Washakius* it appears convincing that the molar metastylids are homologous. Judged from the cheek teeth, both *Shoshonius* and *Washakius* have somewhat divergent specializations. Unlike the apparently *de novo* hypocone off the distolingual corner of the molars of *Washakius*, *Shoshonius* has only the well-developed, probably primitive omomyid protocone-fold.

Contrary to what Simpson stated (1959, p. 154), the construction of M_3 talonid is not the only character of the lower molars that differentiates this genus from *Washakius*. The trigonids of M_2 and M_3 of *Shoshonius* are usually mesiodistally long and the paraconids and metaconid are well separated, whereas in *Washakius* the trigonid is more constricted.

Adaptations. This is a dentally poorly known genus; we know nothing, for example, of the teeth anterior to P_3.

In addition to a combination of crenulated enamel, *Shoshonius* has a metastylid, broad talonids, very extensive buccal cingula coupled with robust mesostyles, and metacones on the third and fourth upper premolars.

Evidence is needed on the anterior dentition before a reliable assessment may be made of its feeding adaptations. Yet the combination of characters, particularly the derived character states, suggest some phytophagous specializations.

Shoshonius cooperi Granger, 1910
Figures 85-89; Table 20

Shoshonius cooperi Granger, 1910, p. 249.

Type. AMNH 14664, maxilla fragment with P^3-M^3; collected from Lost Cabin beds, Alkali Creek, Wind River Formation, northwest of Arminto, Wyoming.

Hypodigm. The type and AMNH 14665, 14668, 14669, 14760, CM 22105, PU 13443, and 18276, all collected from Lost Cabin beds at Alkali Creek; UCM 27342 and AMNH 55153 were collected from Huerfano locs. IV and II, respectively, lower Huerfano Formation.

Geographical and Temporal Distribution. Same as for genus.

Specific Diagnosis. Only known species of genus.

Dental Formula. $I^{?,?}_{?,?}$; $C^{?}_{?}$; $P^{?,3,4}_{?,3,4}$; $M^{1,2,3}_{1,2,3}$, probably as in *Washakius insignis*.

Discussion. Presence of the metastylid in *Shoshonius cooperi* is variable to the extent that it may be nearly absent on all of the molars, e.g., AMNH 55153 ($M_{1\text{-}3}$). On M_1 of AMNH 14669 (Lost Cabin) the metastylid is very small compared to that on M_2. Robinson (1966) did not note the condition of the metastylid on AMNH 55153, a specimen that he referred to *Shoshonius cooperi*. Although the metastylid appears absent, close examination reveals that on the appropriate area of the lingual profile of the trigonids there is barely perceptible relief, showing that this cuspule was poorly developed. The specimen is almost certainly *Shoshonius cooperi*.

The apparent (but not real) differences of the manner in which the cristid obliqua joins the trigonid in AMNH 55153 in contrast to UCM 27342 and AMNH 14665, 14668, 14669, etc., is due to heavy wear on AMNH 55153. Postvallid shear had worn off part of the posterior wall of the trigonid, resulting in an apparently more lingual connection of the cristid obliqua to the trigonid.

Guthrie (1971) recently figured CM 22105 which shows P_3 and P_4 for the first time (see also fig. 89 of present paper).

WASHAKIUS LEIDY, 1873

Washakius Leidy, 1873, p. 123.
Hemiacodon: Wortman, 1904, p. 138.
Yumanius Stock, 1938, p. 288.
Shoshonius?: Simpson, 1959, p. 153.

Type Species. *Washakius insignis* Leidy, 1873.

Included Species. Type species and *Washakius woodringi* (Stock, 1938).

Geographical and Temporal Distribution. Bridgerian to Uintan (medial to late Eocene) of Wyoming and California, respectively.

TABLE 20
Numerical Data for Specimens of *Shoshonius cooperi* from Lost Cabin Beds

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P^3								
L	1	1.70	–	–	–	–	–	–
AW	1	2.13	–	–	–	–	–	–
L/AW	1	0.80	–	–	–	–	–	–
P^4								
L	2	1.60-1.70	–	–	–	–	–	–
AW	2	2.35-2.42	–	–	–	–	–	–
L/AW	2	0.68-0.70	–	–	–	–	–	–
M^1								
L	2	1.80-2.05	–	–	–	–	–	–
AW	2	2.70-2.75	–	–	–	–	–	–
L/AW	2	0.65-0.76	–	–	–	–	–	–
M^2								
L	2	1.40-1.95	–	–	–	–	–	–
AW	2	3.00-3.25	–	–	–	–	–	–
L/AW	2	0.43-0.65	–	–	–	–	–	–
M^3								
L	3	1.75	–	1.750	–	–	–	–
AW	3	2.60-2.72	0.0	2.673±0.037	0.064±0.026	2.605±1.064	–	–
L/AW	3	0.64-0.67	–	0.655±0.009	0.016±0.007	2.638±1.077	–	–
M_1								
L	4	2.00-2.15	–	2.050±0.035	0.071±0.025	3.665±1.296	1.414	1.500
PW	4	1.60-1.78	−0.599	1.657±0.041	0.083±0.029	5.296±1.872	1.862	3.579
AW	4	1.50-1.60	−0.816	1.550±0.029	0.058±0.020	3.958±1.399	0.000	−6.000
L/PW	4	1.12-1.34	–	1.240±0.046	0.092±0.032	7.843±2.773	−0.384	0.743
M_2								
L	6	2.00-2.10	–	2.025±0.017	0.042±0.012	2.152±0.621	1.537	1.429
PW	6	1.63-1.85	−0.028	1.753±0.035	0.086±0.025	5.106±1.474	−0.106	−0.937
AW	6	1.60-1.80	−0.057	1.687±0.034	0.084±0.024	5.177±1.494	0.279	−2.273
L/PW	6	1.08-1.24	–	1.570±0.025	0.062±0.018	5.612±1.620	0.307	−1.608
M_3								
L	6	2.50-2.70	–	2.597±0.032	0.079±0.023	3.176±0.917	0.348	−1.633
PW	6	1.40-1.70	0.524	1.563±0.048	0.117±0.034	7.789±2.249	−0.127	−1.454
AW	6	1.40-1.68	0.765	1.572±0.040	0.099±0.029	6.553±1.892	−1.142	1.265
L/PW	6	1.53-1.79	–	1.667±0.044	0.107±0.031	6.694±1.932	0.047	−1.973

Generic Diagnosis. Omomyids which differ from other genera in having a combination of metastylid, double metaconule, and the distinct, cuspate hypocone broadly based on the distal cingulum. *Washakius* differs from *Shoshonius*, probably its near ancestor, in having robust parastyles on the third and fourth premolars and lacking the small metacone of the latter on these teeth.

Discussion. Gazin (1958, pp. 57-62) thoroughly treated this genus, giving detailed descriptions for all the pertinent material for *Washakius insignis* and allocating *Yumanius woodringi* Stock, 1938, to *Washakius*.

Relatively little or no controversy exists as to the closest relationships of this genus within the Omomyidae. The comparisons by Gazin have been with *Shoshonius*, *Omomys*, and *Hemi-*

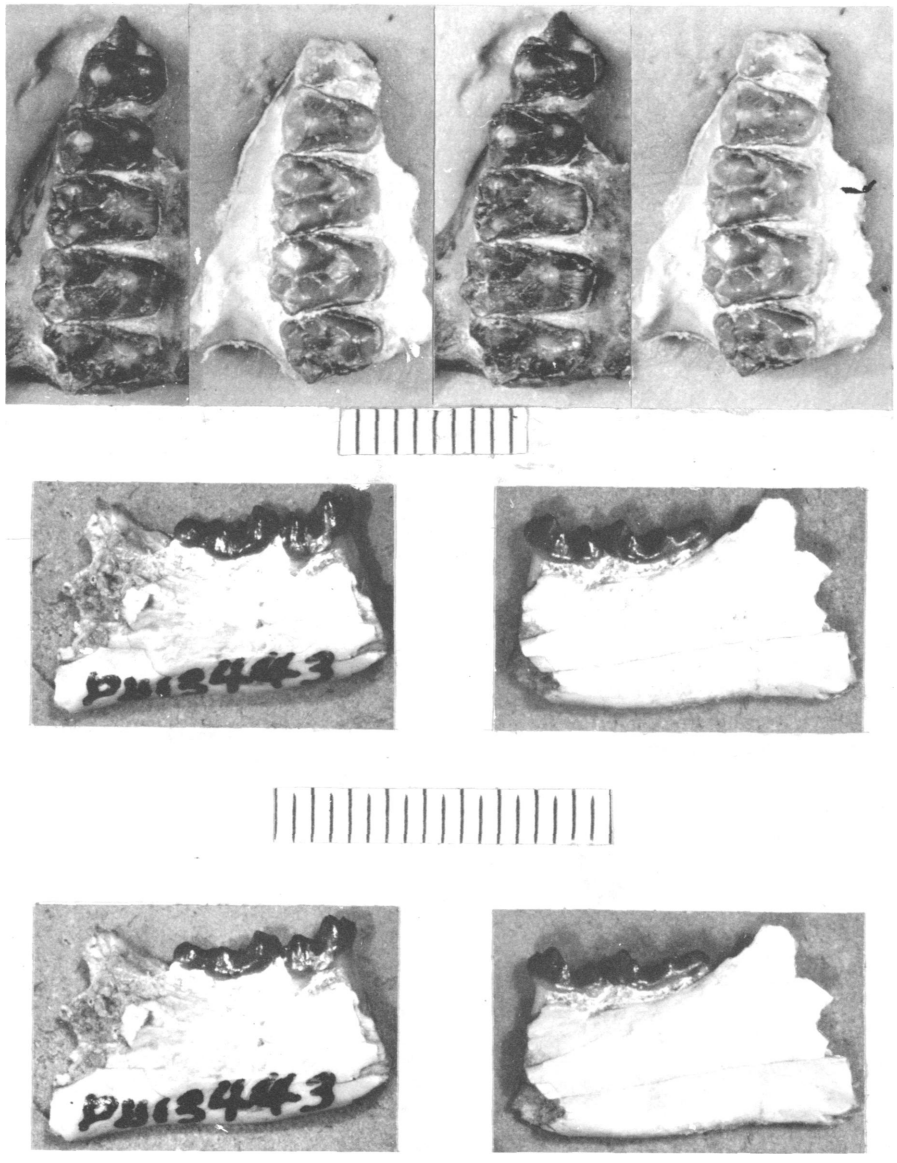


FIG. 85. *Shoshonius cooperi*, AMNH 14664, type, right P^3-M^3 (above left); PU 13443, right P^4-M^3 (above right); and PU 13443, right M_{1-3} (below); all from Lost Cabin beds. Stereophotographs: above occlusal, below left lateral, and below right medial views. Subdivisions on scales represent 0.5 mm.

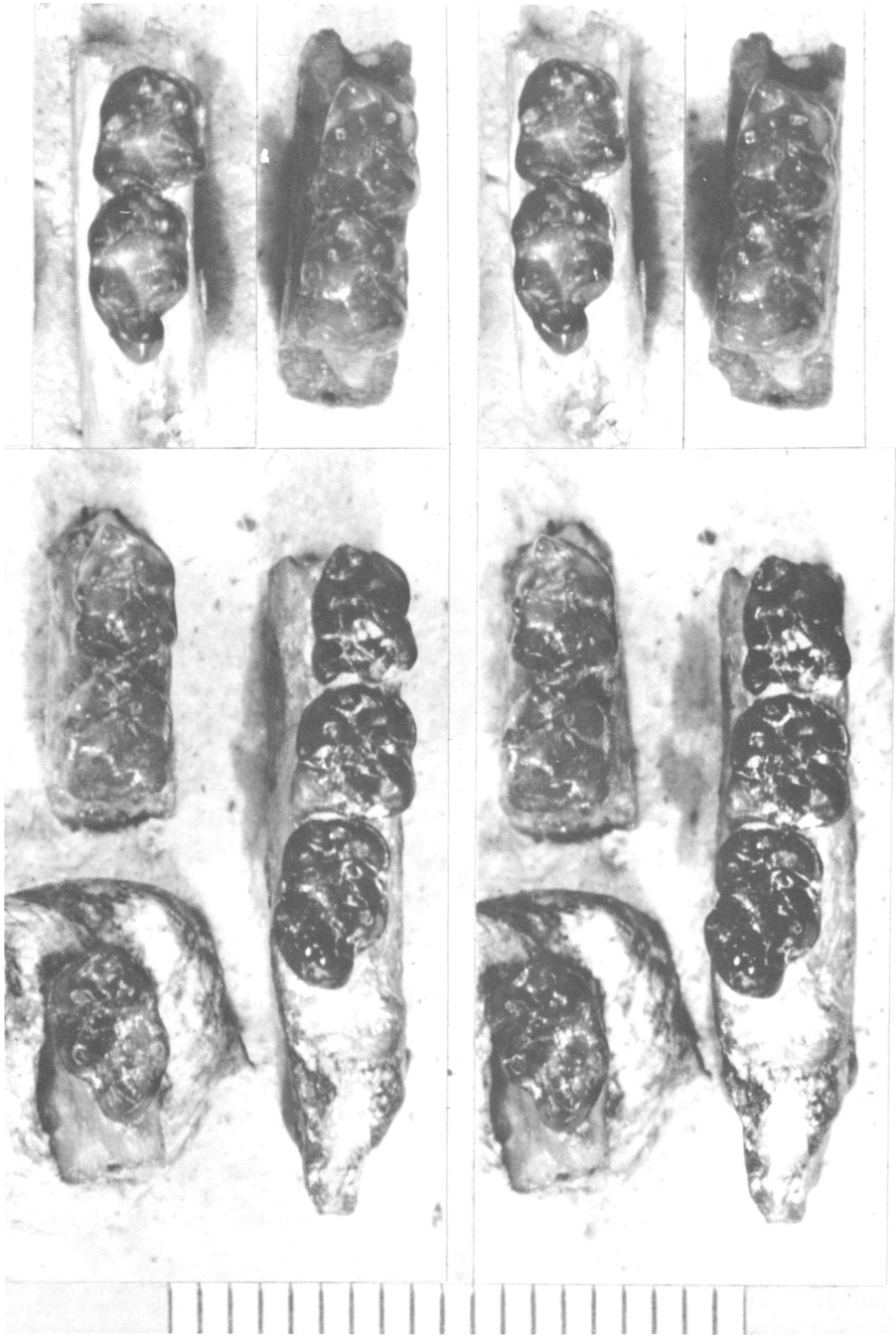


FIG. 86. *Shoshonius cooperi*, part of PU 13443, right M_{2-3} (above left); AMNH 14669, right M_{1-2} (middle left); AMNH 14670, left M_3 (below left); AMNH 14668, right M_{1-2} (above right); and AMNH 55153, right M_{1-3} (below right); all from Lost Cabin beds. Stereophotographs: all occlusal views. Subdivisions on scale represent 0.5 mm.

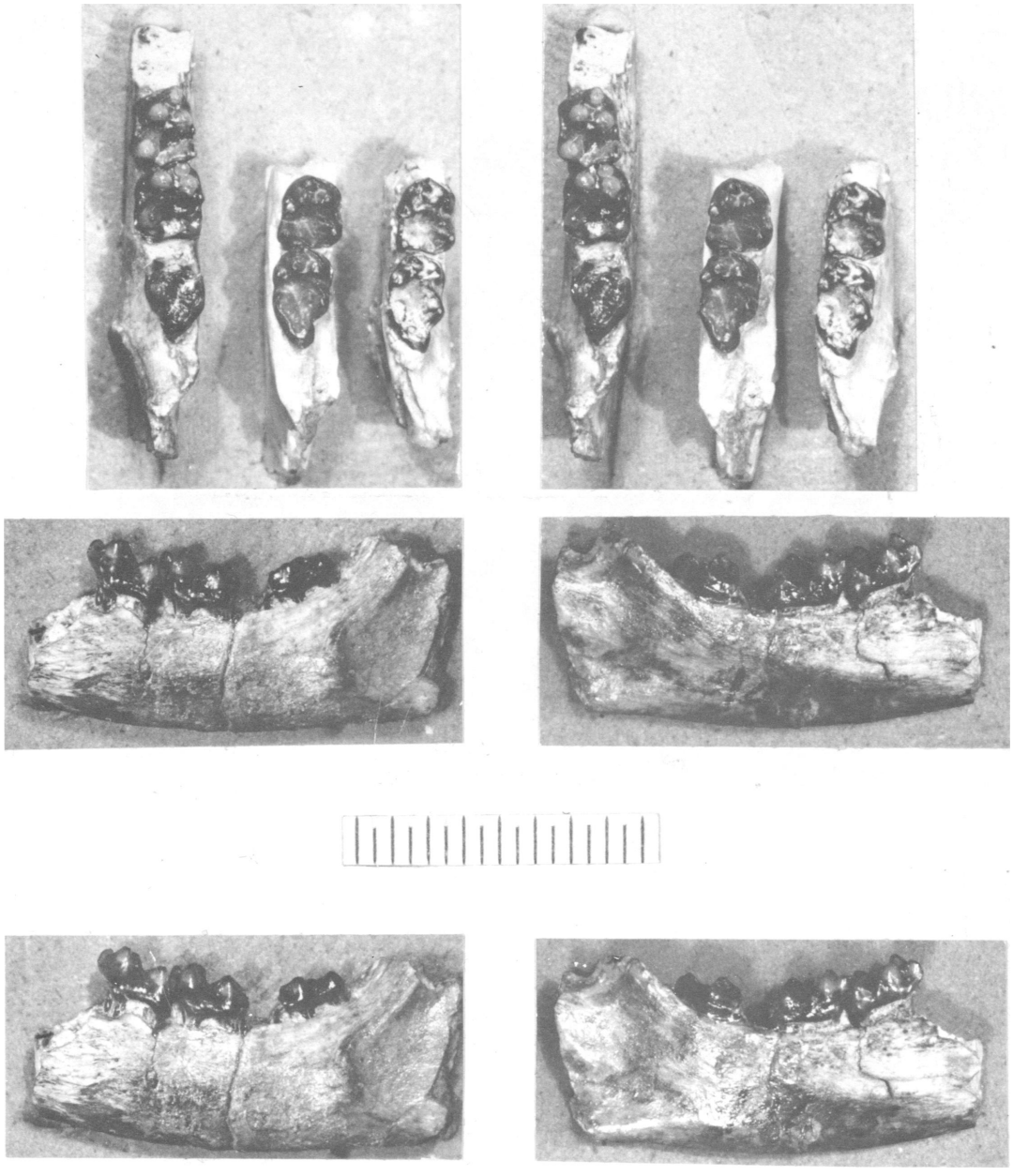


FIG. 87. *Shoshonius cooperi*, AMNH 14665, left M_{1-3} (above left and below) and PU 13443, two specimens of right M_{2-3}, both from Lost Cabin beds. Stereophotographs: above occlusal, below left lateral, and below right medial views, respectively. Subdivisions on scale represent 0.5 mm.

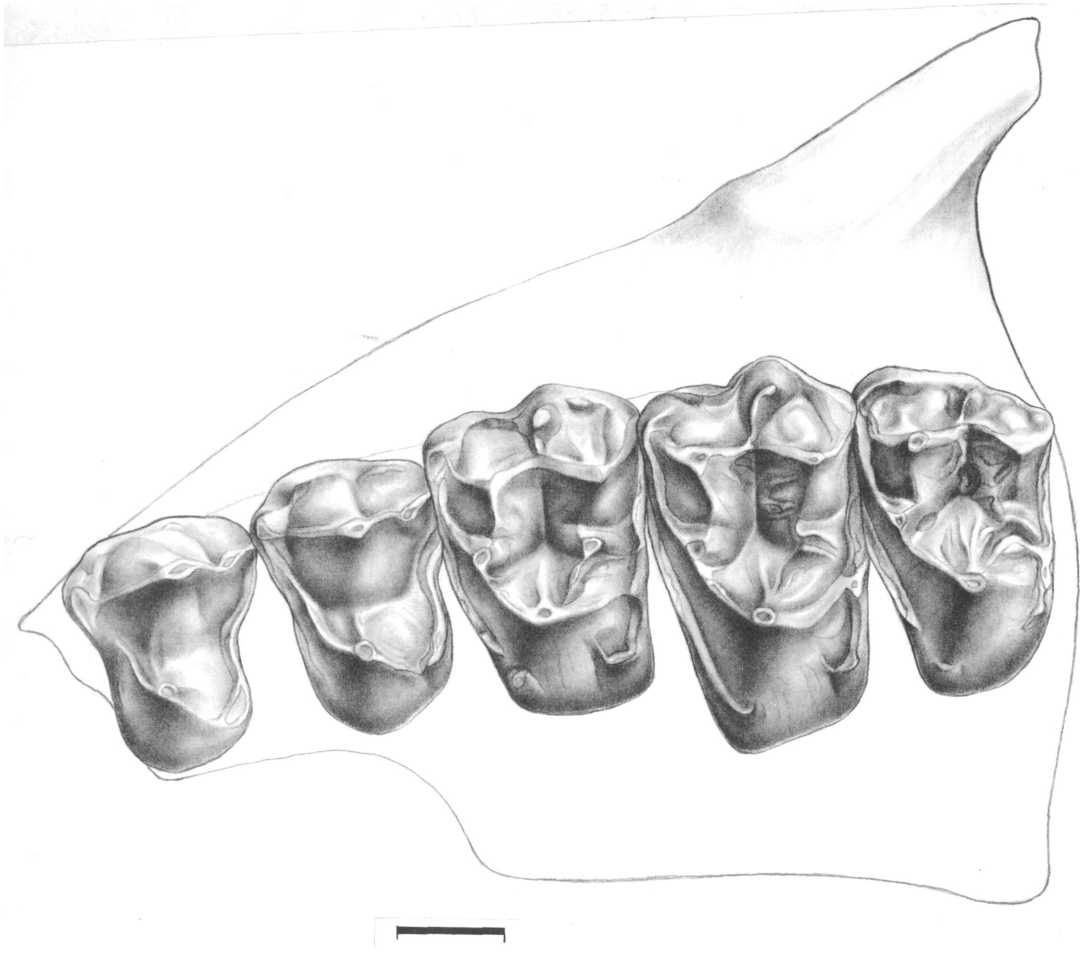


FIG. 88. *Shoshonius cooperi*, right P^3-M^3, based primarily on AMNH 14664, type, late Wasatchian of Wyoming and Colorado; occlusal view. Scale represents 1 mm.

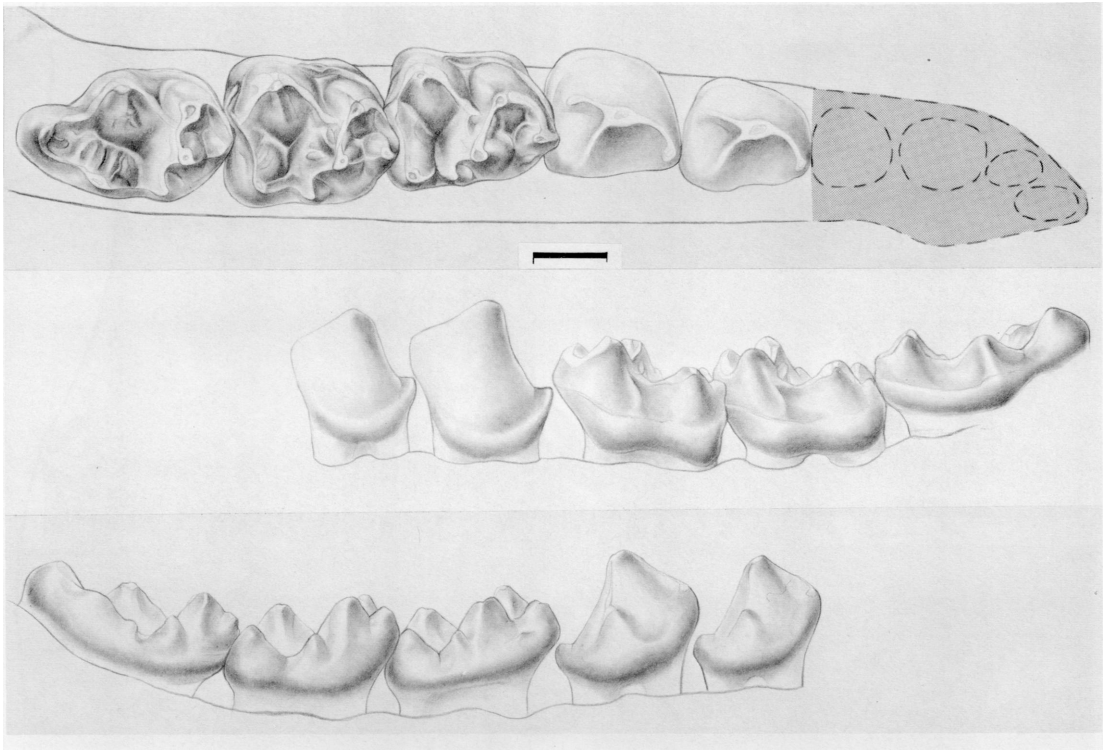


FIG. 89. *Shoshonius cooperi*, left P_3-M_3, based on AMNH 14665 and CM 22105, late Wasatchian of Wyoming and Colorado; occlusal (above), buccal (middle), and lingual (below) views. Reconstruction shown by uniform stippling and broken lines. Scale represents 1 mm.

acodon, and Simpson's (1940, p. 189) suggestion of its close ties to *Loveina* has been accepted by Gazin (1958, chart 1). Gazin's allocation of *Yamanius* to *Washakius* has been followed by Russell, Louis, and Savage (1967, fig. 14), and I also believe this to be desirable pending further discoveries of *Yumanius* specimens. As I stated under the generic discussions of *Loveina* and *Shoshonius*, these two taxa are probably the most recently related and the most closely resembling *Washakius*.

The distinct possibility exists that *W. woodringi* shares a more recent ancestor with *Dyseolemur pacificus* than with *W. insignis*. Were this to be confirmed in the future by better samples of the Californian taxa, it may necessitate, if not inclusion of *Dyseolemur* in *Washakius*, then referral of Stock's species to *Dyseolemur*. Much as I suspect this genealogy to be correct, nothing is gained at present in transferring *Yumanius woodringi* from *Washakius* to *Dyseolemur* as the mere two teeth of *W. woodringi* can be argued to show closer ties with either.

Adaptations. The major specializations of *Washakius* are in the presence of metastylids, greatly elongated M_3 talonid, large conules on the upper molars, an additional metaconule, well-developed hypocones, cingula and cingulids, and robust parastyles on the two known upper premolars P^3 and P^4. The lower P_2 and canine and the alveoli of P^2 and the upper canine show transversely widened teeth, clearly a specialization. In stark contrast to this the incisors were clearly of lesser importance than in most omomyids. Interestingly, among the molars of many specimens of *Washakius insignis* a large number are relatively well worn, and some show the extreme conditions of attrition (fig. 93).

The combined evidence of the dentition together with the somewhat enlarged angle of the

mandible strongly indicate that *Washakius insignis* was a herbivore, and in particular a small specialized folivore.

The little we know of *Washakius woodringi*, however, does not necessarily reflect adaptations to folivory. Although the primitive (?) features of this species clearly reflect an ancestry like *Washakius insignis*, the high, pointed cusps suggest adaptations to a more insectivorous diet.

Washakius insignis Leidy, 1873
Figures 90-99; Table 21

Washakius insignis Leidy, 1873, p. 123.
Hemiacodon pygmaeus Wortman, 1904, p. 138.
Shoshonius ?laurae Simpson, 1959, p. 153.

Type. Right mandible fragment with M_{2-3}, in Philadelphia Academy of Sciences; collected from Bridger beds (for illustration see fig. 23a in Osborn, 1902, p. 200).

Hypodigm. The type, and AMNH 12038, 12039, 12040, 12605-6, 12607, 13035, 13240-1, YPM 13235-2, 13235-4, 13236-1, 14658, all from various, mostly unknown, Bridger localities; UW 1645, AMNH 55672, from Morrow Creek loc. 10 (lower Bridger beds); AMNH 55665, 55668, 56037, and MCZ 17944, from Tabernacle Butte loc. 5, Bridger beds, Bridger Basin, Wyoming.

Geographical and Temporal Distribution. Bridgerian (medial Eocene) of Wyoming.

Specific Diagnosis. Differs from *W. woodringi* in having slightly lower, blunter cusps and a less distinct protocone-fold.

Dental Formula. $I\frac{1,2}{1,2}; C\frac{1}{1}; P\frac{2,3,4}{2,3,4}; M\frac{1,2,3}{1,2,3}$.

Discussion. With the exception of the description of *Shoshonius ?laurae* by Simpson (1959) there have been no taxonomic problems associated with this species. Simpson based the species on AMNH 55672, a left mandible with M_{1-3}. Contrary to what Simpson has stated, M_3 is not closely similar to that of *Shoshonius cooperi*. The trigonid is mesiodistally constricted as in other *Washakius insignis* specimens, and, as in the latter again, the twinned hypoconulid clearly allies this specimen with this species. The relatively large size of the M_3 talonid is a considerably variable feature (see figs. 92-95). The type of "*Shoshonius laurae*," contary to Simpson's statement, could not be easily referred to either *Washakius*, *Shoshonius*, or *Dyseolemur*. I refer it with confidence to *W. insignis*.

Washakius woodringi (Stock, 1938)
Figures 69, 100

Yumanius woodringi Stock, 1938, p. 288.
Washakius woodringi (Stock, 1938) Gazin, 1958, p. 62.

Type. LACM 2233, right maxilla fragment with M^{1-2}, collected from white sandstones associated with the Poway conglomerate and exposed on the west bank of San Diego River, approximately ¼ mile north and east of San Diego Mission, CIT Vert. Paleo. loc. 249.

Hypodigm. Type specimen only.

Geographical and Temporal Distribution. Uintan (late Eocene) of California.

Specific Diagnosis. Differs from the genero-type in having more pointed cusps, and a well-developed protocone-fold.

Dental Formula. Probably the same as for *W. insignis*.

Discussion. The following are measurements in millimeters of the type of *Washakius woodringi*: LM^1, 1.92; WM^1, 2.63; LM^2, 1.84; WM^2, 2.86.

As mentioned under the genus, I am uncertain concerning the referral of this species to *Washakius*. A larger sample may eventually show a number of synapomorphies with *Dyseolemur* and not with *Washakius*. If this species and *Dyseolemur pacificus* share a number of derived characters, allocation of this species to *Dyseolemur* may become necessary. An eventual return to the use of *Yumanius* is obviously not excluded as a possibility, pending a new and adequate sample.

DYSEOLEMUR STOCK, 1934

Dyseolemur Stock, 1934, p. 150.

Type Species. Dyseolemur pacificus Stock, 1934.

Included Species. Type species only.

Geographical and Temporal Distribution. Uintan (late Eocene) of California.

Generic Diagnosis. Omomyids that differ from all others except *Shoshonius*, Washakius, and

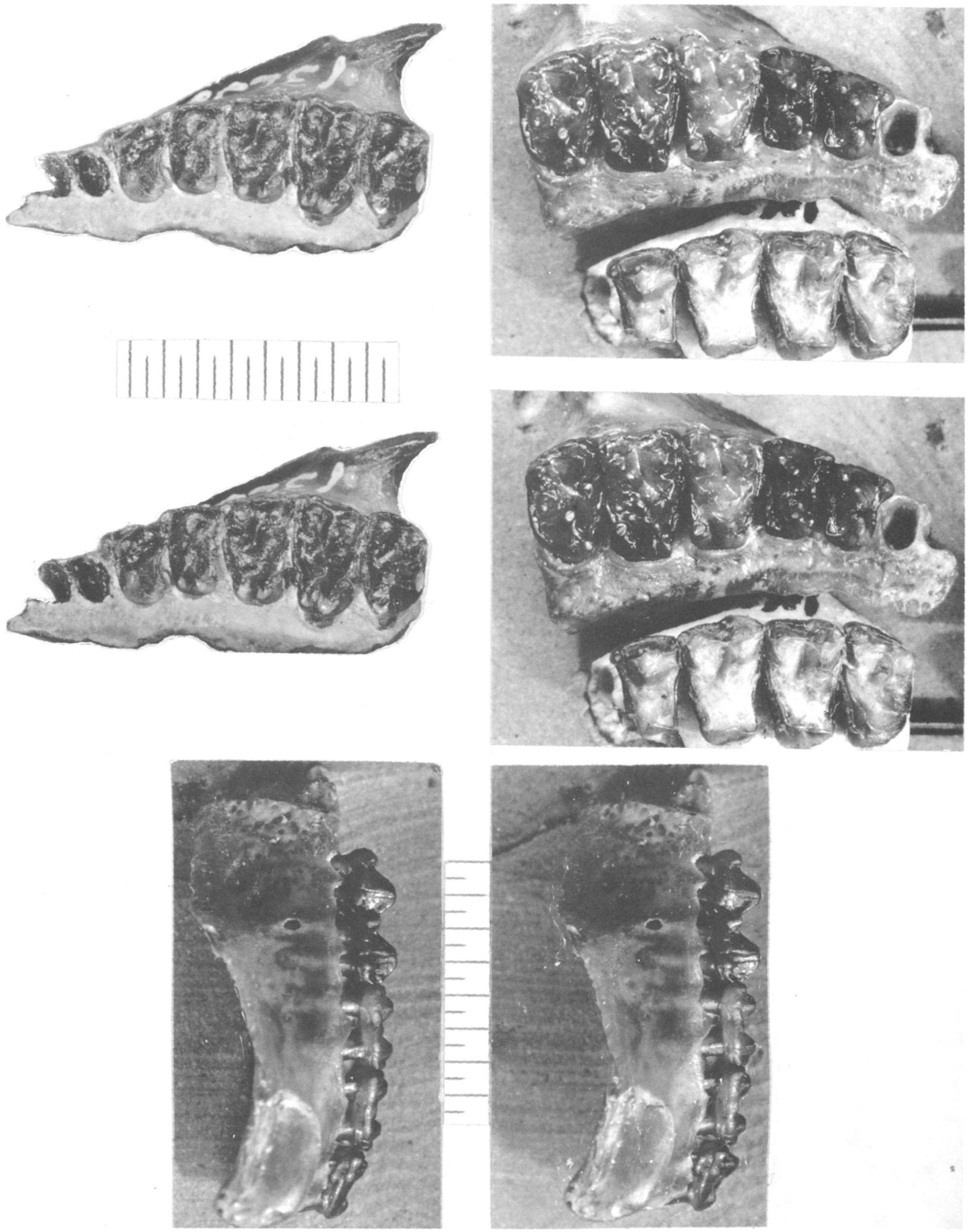


FIG. 90. *Washakius insignis*, YPM 13235-4, left P^3-M^3 (above left); AMNH 56037, right P^3-M^3 (above right and below); AMNH 55665, left P^4-M^3 (second row right); all from Bridger beds. Stereophotographs: above occlusal and below lateral views. Subdivisions on scales represent 0.5 mm.

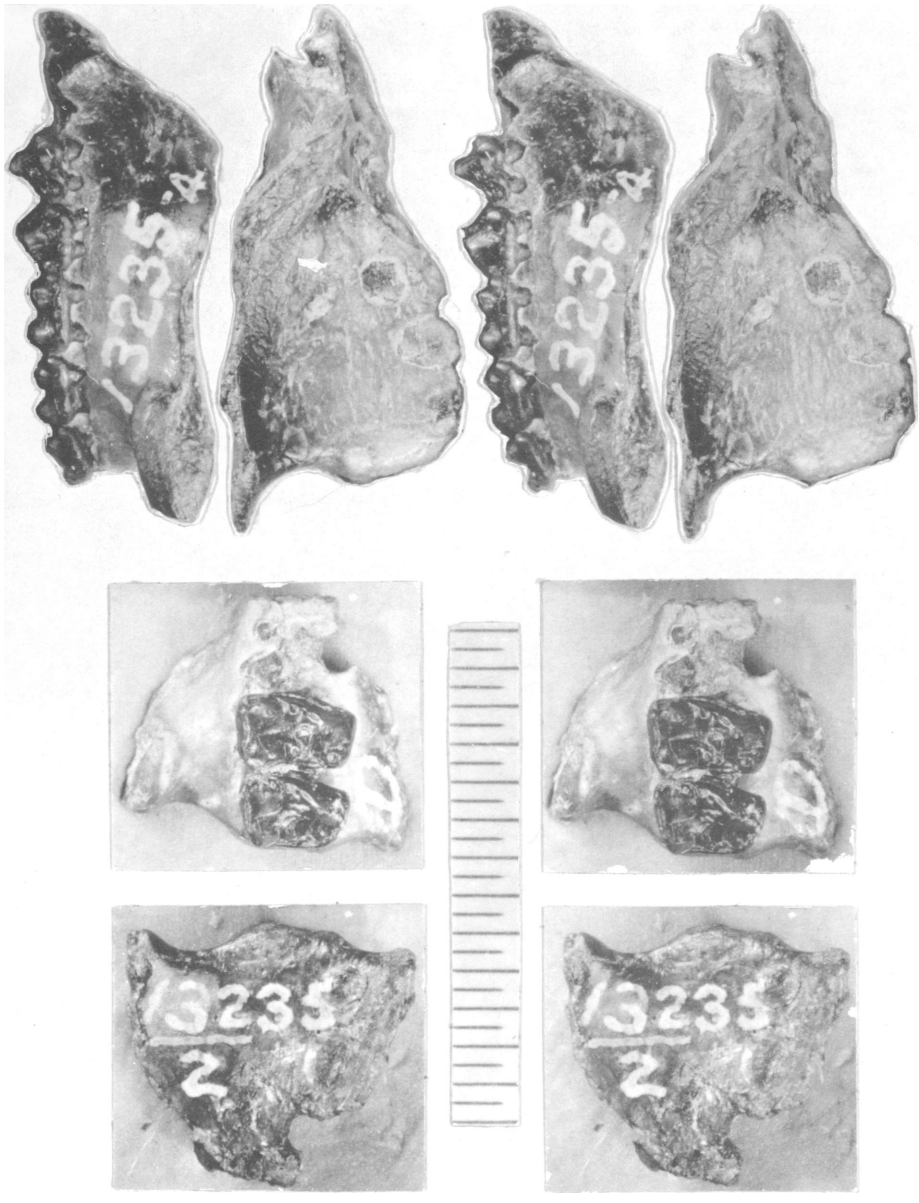


FIG. 91. *Washakius insignis*, YPM 13235-4, left P^3-M^3 (above), and AMNH 13235-2, right M^{2-3} (middle and below); all from Bridger beds. Stereophotographs: above left lateral, above right and below dorsal, and middle occlusal views. Subdivisions on scale represent 0.5 mm.

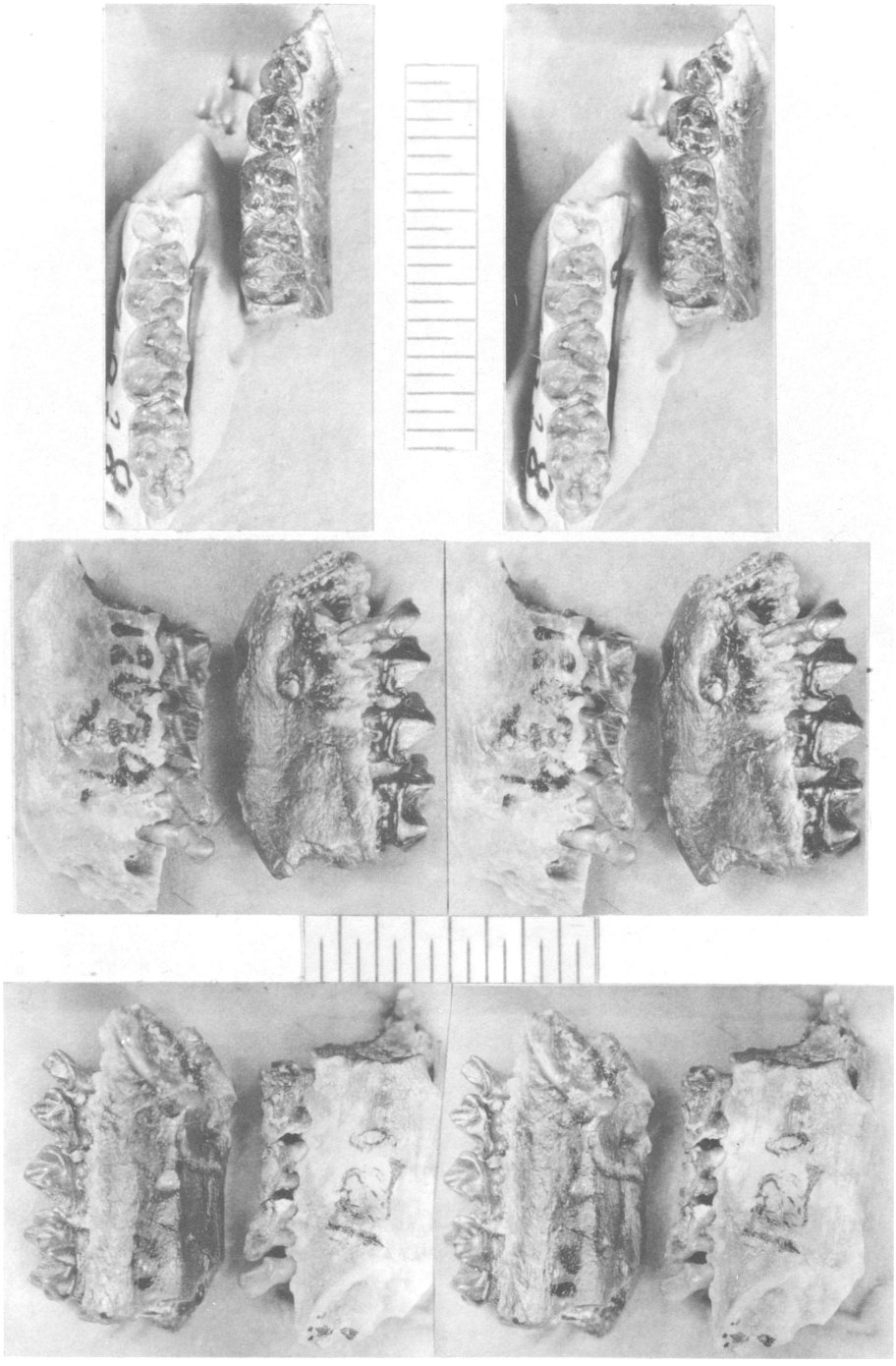


FIG. 92. *Washakius insignis*, AMNH 12038, left M_{1-3} (above left); AMNH 12040, left P_2-M_1 (above right, middle right, and below left); AMNH 12039, right P_2-M_1 (middle left and below right); all from Bridger beds. Stereophotographs: above occlusal, middle lateral, and below medial views. Subdivisions on scales represent 0.5 mm.

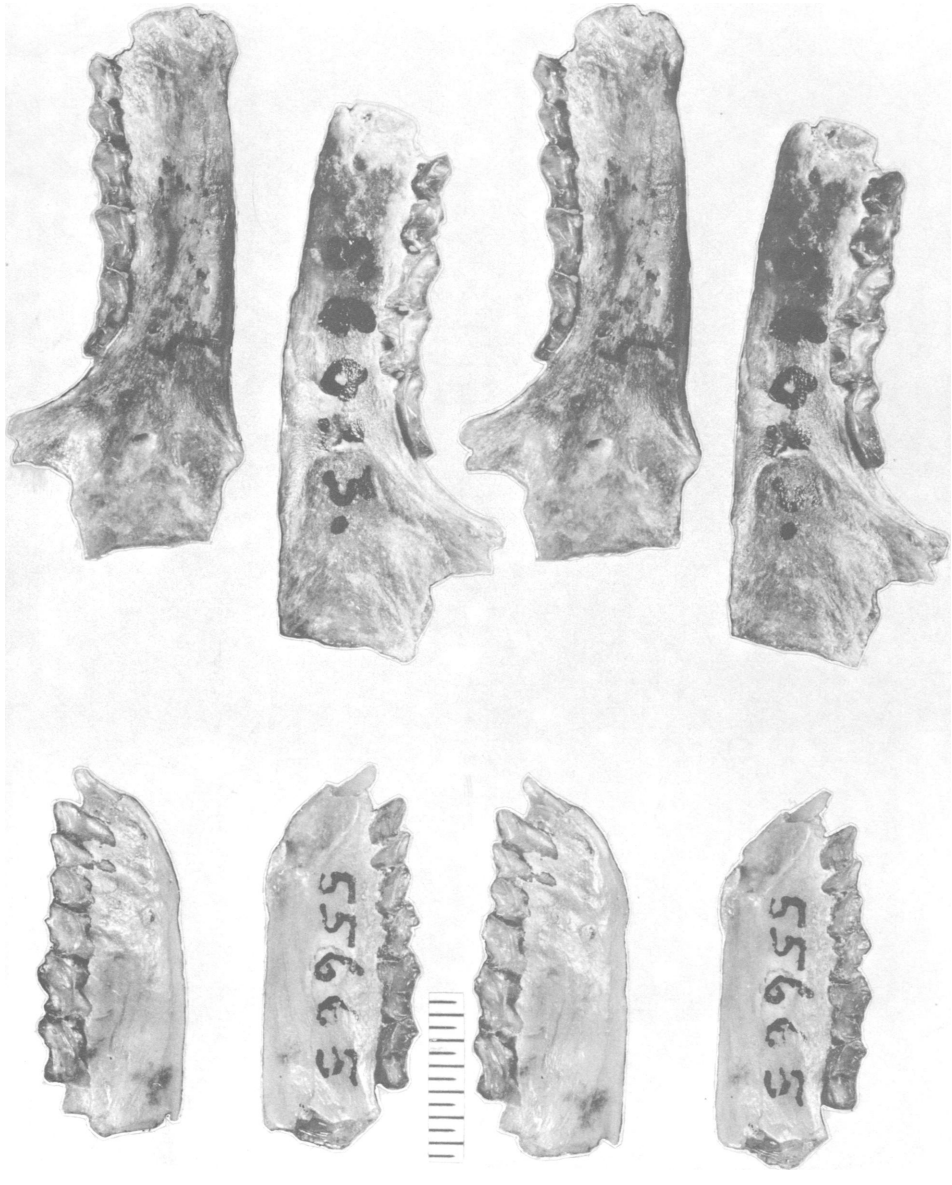


FIG. 93. *Washakius insignis*, AMNH 56033, left P_3-M_3 (above) and AMNH 55665, right C-M_2 (below), both from Bridger beds. Stereophotographs: above left and below left lateral and above right and below right medial views. Subdivisions on scale represent 0.5 mm.

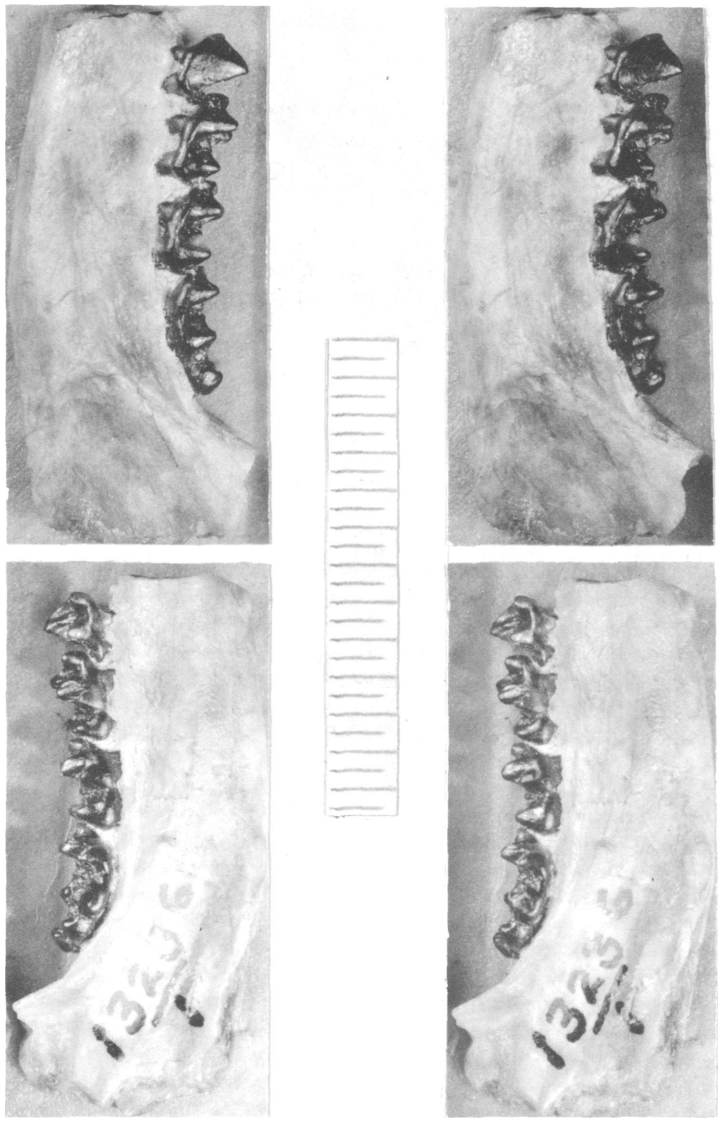


FIG. 94. *Washakius insignis*, YPM 13236-1, Bridger beds, left P_4-M_3. Stereophotographs: above lateral and below medial views. Subdivisions on scale represent 0.5 mm.

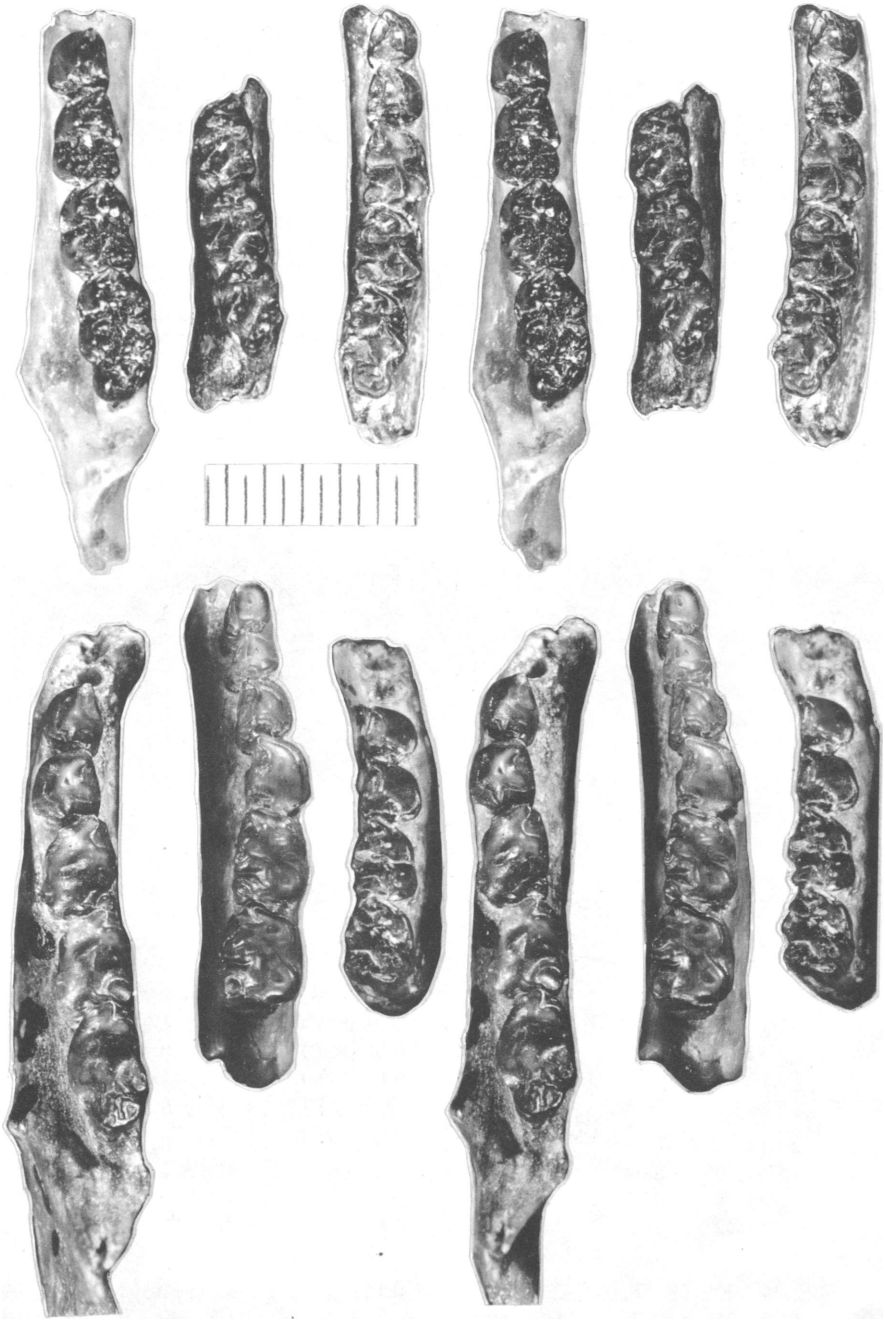


FIG. 95. *Washakius insignis*, YPM 13236-1, left P_4-M_3 (above left); AMNH 55672, type of "*Shoshonius*? *laurae*," left M_{1-3} (above center); UW 1645, right P_3-M_3 (above right); AMNH 56033, left P_3-M_3 (below left); AMNH 55665, right C-M_2 (below center); and YPM 14658, right P_3-M_2 (below right); all from Bridger beds. Stereophotographs: all occlusal views. Subdivisions on scale represent 0.5 mm.

TABLE 21
Numerical Data for Specimens of *Washakius insignis* from Bridger Beds

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P^3								
L	1	1.75	–	–	–	–	–	–
AW	1	2.25	–	–	–	–	–	–
L/AW	1	0.78	–	–	–	–	–	–
P^4								
L	1	1.75	–	–	–	–	–	–
AW	1	2.45	–	–	–	–	–	–
L/AW	1	0.71	–	–	–	–	–	–
M^1								
L	1	2.05	–	–	–	–	–	–
AW	1	2.55	–	–	–	–	–	–
L/AW	1	0.80	–	–	–	–	–	–
M^2								
L	2	1.95-2.00	–	–	–	–	–	–
AW	2	3.00-3.10	–	–	–	–	–	–
L/AW	2	0.65	–	–	–	–	–	–
M^3								
L	2	1.80-1.90	–	–	–	–	–	–
AW	2	2.70-2.80	–	–	–	–	–	–
L/AW	2	0.64-0.70	–	–	–	–	–	–
P_3								
L	1	1.40	–	–	–	–	–	–
PW	1	1.25	–	–	–	–	–	–
L/PW	1	1.12	–	–	–	–	–	–
P_4								
L	2	1.65-1.82	–	–	–	–	–	–
PW	2	1.47-1.50	–	–	–	–	–	–
L/PW	2	1.12-1.21	–	–	–	–	–	–
M_1								
L	9	2.10-2.30	–	2.200±0.022	0.066±0.016	3.090±0.728	−0.416	−0.198
PW	9	1.50-1.75	0.380	1.620±0.027	0.082±0.019	5.203±1.226	0.213	−0.774
AW	9	1.50-1.70	0.653	1.611±0.022	0.065±0.015	4.152±0.979	−0.083	−0.189
L/PW	9	1.26-1.47	–	1.360±0.022	0.065±0.015	4.899±1.155	0.000	−0.139
M_2								
L	8	2.10-2.30	–	2.202±0.021	0.060±0.015	2.818±0.704	−0.159	0.682
PW	8	1.70-1.80	0.444	1.750±0.009	0.027±0.007	1.575±0.394	0.000	3.500
AW	8	1.60-1.79	0.370	1.720±0.020	0.057±0.014	3.422±0.855	−1.353	2.666
L/PW	8	1.20-1.29	–	1.259±0.011	0.031±0.008	2.554±0.639	−0.981	0.508
M_3								
L	6	2.75-3.20	–	2.967±0.064	0.157±0.045	5.515±1.592	0.120	−0.034
PW	6	1.70-1.75	0.305	1.713±0.009	0.022±0.006	1.313±0.379	1.323	0.214
AW	6	1.60-1.85	0.678	1.658±0.040	0.097±0.028	6.095±1.760	2.116	4.678
L/PW	6	1.59-1.83	–	1.731±0.035	0.087±0.025	5.219±1.507	−0.838	0.175

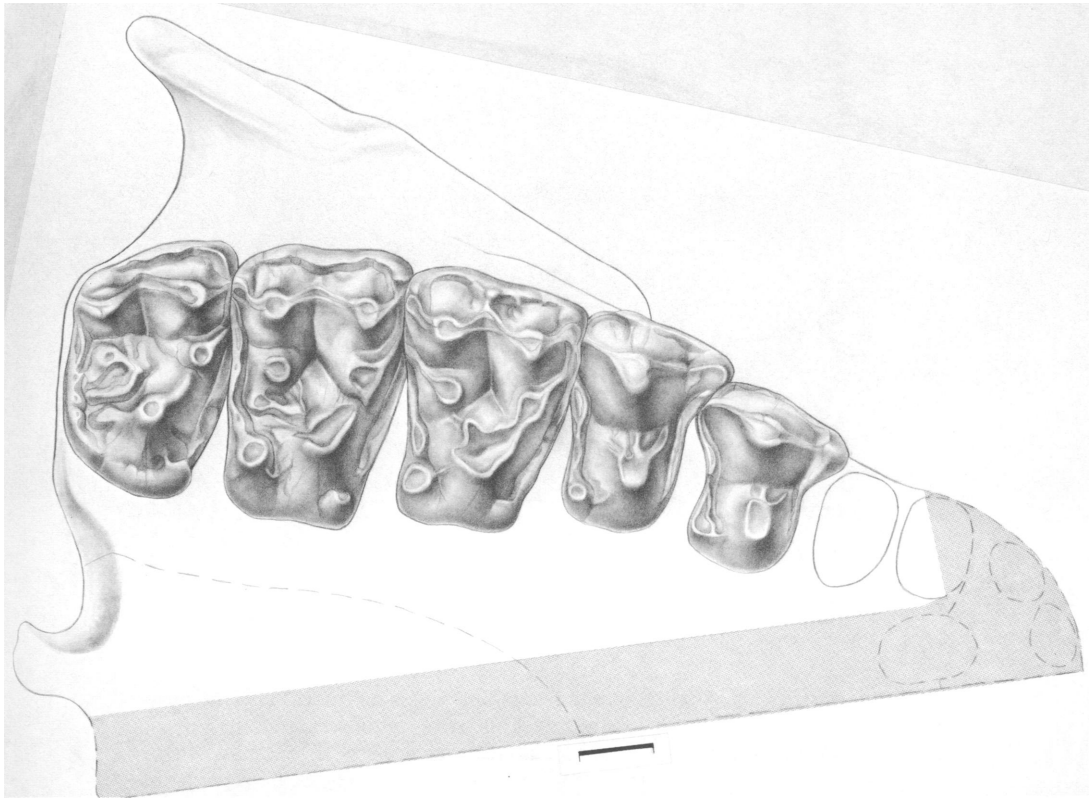


FIG. 96. *Washakius insignis*, right P^3-M^3, based on AMNH 55665, 55672, and 56037, YPM 13236-1 and 15019, Bridgerian of Wyoming; occlusal view. Reconstruction shown by uniform stippling and broken lines. Scale represents 1 mm.

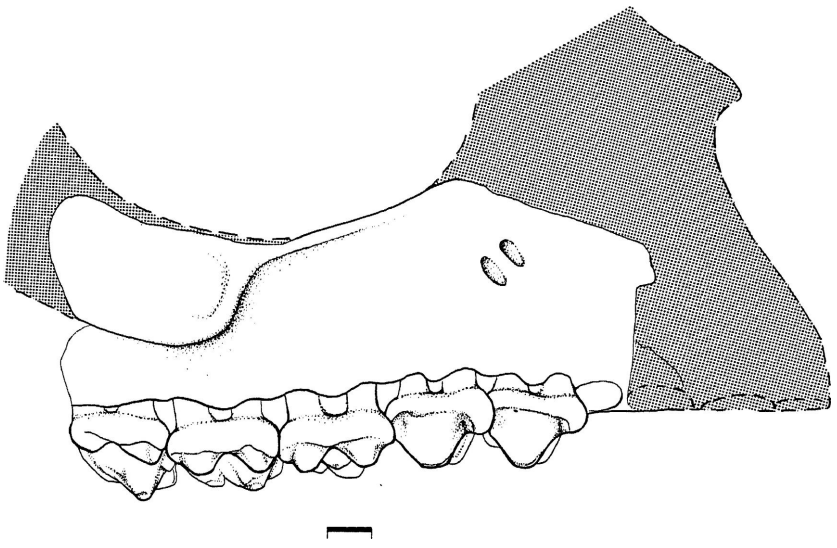


FIG. 97. *Washakius insignis*, maxilla fragment showing buccal view of cusp relief on teeth with part of the muzzle and orbit reconstructed, based on AMNH 56037, Bridgerian of Wyoming; lateral (and somewhat occlusal) view. Reconstruction shown by uniform stippling and broken lines. Scale represents 1 mm.

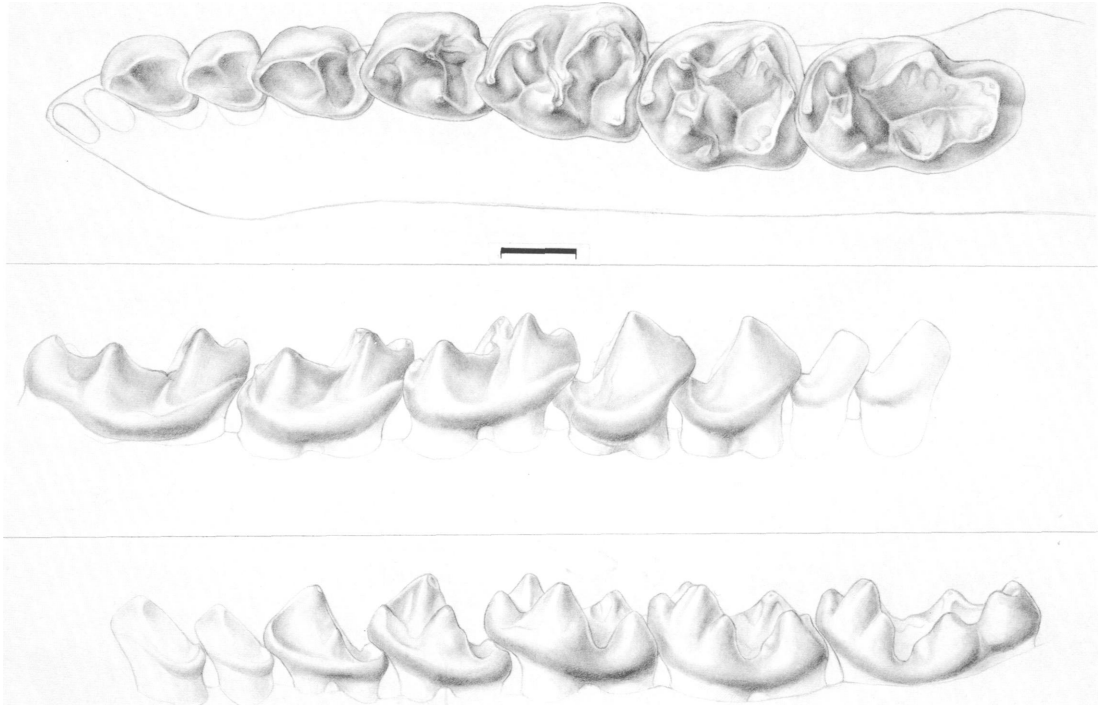


FIG. 98. *Washakius insignis*, right C-M_3, based on AMNH 12040, UW 1645 and 55665, Bridgerian of Wyoming; occlusal (above), buccal (middle), and lingual (below) views. Scale represents 1 mm.

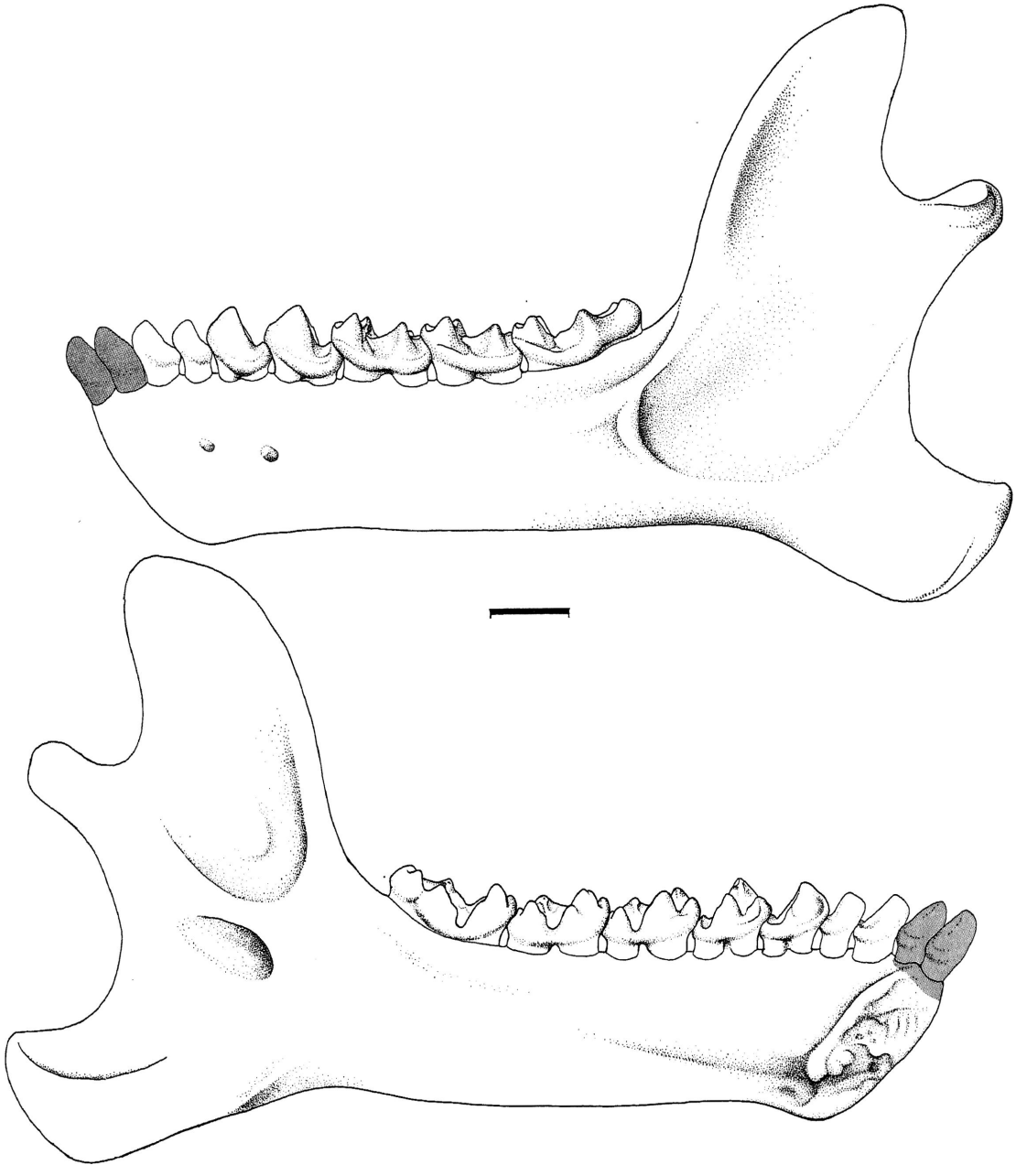


FIG. 99. *Washakius insignis*, reconstructed left mandible based on known hypodigm, Bridgerian of Wyoming; lateral (above) and medial (below) views. Missing parts shown by uniform stippling. Scale represents 1 mm.

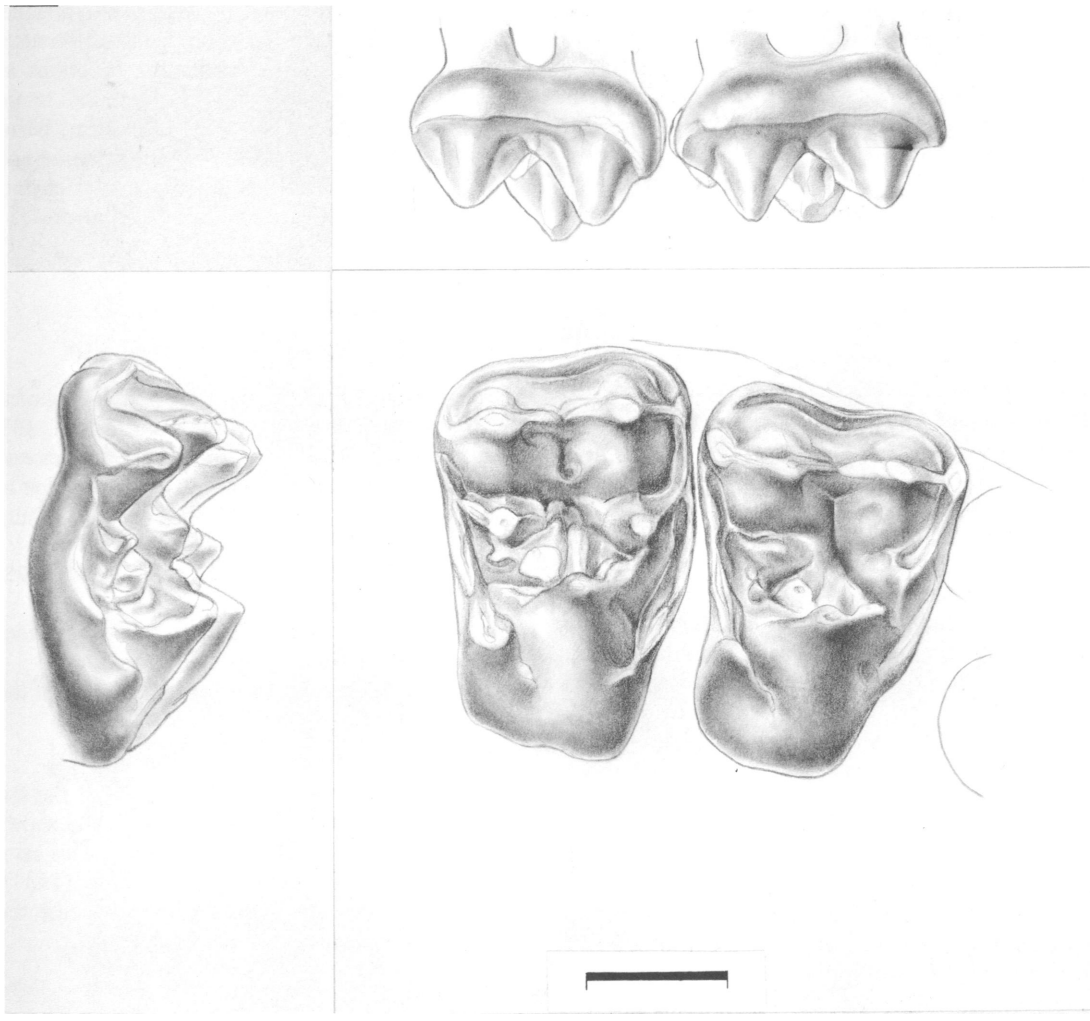


FIG. 100. *Washakius woodringi*, LACM 2233, Uintan of California, right M^{1-2}; buccal (above), distal (below left), and occlusal (below right) views. Scale represents 1 mm.

Ekgmowechashala in the possession of a metastylid. *Dyseolemur* differs from *Shoshonius* in the absence of the mesostyle and in having a well-developed cingular area distolingually which can be defined as the hypocone. *Dyseolemur* differs from *Washakius* in the apparent absence of the "second" metaconule and particularly in having the paraconid removed to the extreme mesiobuccal corner of the lower tooth. In addition, M_3 tends to be relatively smaller than that in *Washakius*.

Discussion. Stock (1934), when describing *Dyseolemur pacificus*, clearly stated that this taxon was most likely derived from *Washakius*. In discussing *Dyseolemur*, Gazin (1958) affirmed the relatively close ties of the Sespe *Dyseolemur* to *Washakius*. Russell, Louis, and Savage (1967) did the same, showing the derivation of the Uintan *Dyseolemur* directly from *Washakius*, conclusions with which I concur.

Dyseolemur appears to be linked with both *Shoshonius* and *Washakius* in possessing a metastylid, but the other special resemblances are with *Washakius*. The hypocone off the postcingulum is well developed in *Dyseolemur*, as in *Washakius*, and the former, as does the latter, also lacks the mesostyle shown by *Shoshonius*. The talonid notch of *Dyseolemur* is shaped identically with that of *Washakius*, a feature whereby M_1 and M_2 of both may be distinguished from *Shoshonius*.

The trigonid structure of *Dyseolemur* shows specializations beyond those of *Washakius*. The paraconid is in an extreme mesiobuccal position and consequently the paracristid is relatively shorter than that of *Washakius*. Judged by the morphology of M_3 it appears that this relatively shorter tooth of *Dyseolemur* was reduced from a relative size similar to that shown by *Washakius*.

Contrary to what has been stated by Simpson (1959, p. 155), the lower molars of *Dyseolemur* and *Shoshonius* are distinctive. In contrast to those in the latter, which have the primitively long paracristids, in *Dyseolemur* they are very short and do not extend so far lingually as in *Shoshonius*.

Adaptations. Perhaps the somewhat more bunodont cusps (a rather subjective appraisal) of *Dyseolemur*, along with the relatively larger protocone crest and the greater enlargement of the lingual third of the postcingulum as a hypocone, represent the major morphological differences from *Washakius*. The mechanical functions of these characters may have been related to increasing crushing and/or transverse shear. Whatever the differences between *Dyseolemur* and *Washakius*, the gestalt of known dental characters suggest a herbivore, probably a frugivore.

Dyseolemur pacificus Stock, 1934
Figures 69, 101-103; Table 22

Dyseolemur pacificus Stock, 1934, p. 150.

Type. LACM 1395, right mandible fragment with P_4-M_3; collected from Tapo Ranch, CIT Vert. Paleo. loc. 180, approximately 3 miles east of loc. 150 and approximately 700 feet lower in the Sespe deposits, north of Simi Valley, Ventura County, California.

Hypodigm. LACM 1528, 1530, 5191-5195, Tapo Ranch localities.

Geographical and Temporal Distribution. Same as for genus.

Specific Diagnosis. Only known species of the genus.

Dental Formula. $I\frac{1,2}{1,2}$; $C\frac{1}{1}$; $P\frac{2,3,4}{2,3,4}$; $M\frac{1,2,3}{1,2,3}$.

Discussion. Figures 101-103 show all the important specimens known and figure 103 shows how much of the dentition is known. This sample has been described in detail by Stock (1934). The upper teeth are poorly known because the two known specimens are relatively worn.

HEMIACODON MARSH, 1872

Hemiacodon Marsh, 1872, p. 212.
Omomys: Osborn, 1902, p. 173.

Type Species. Hemiacodon gracilis Marsh, 1872.

Included Species. Type species only.

Geographical and Temporal Distribution. Bridgerian (medial Eocene) of Wyoming.

Generic Diagnosis. Omomyines with very heavily folded enamel, a fourth lower premolar subequal in height to the first lower molar, very heavy cingulids on the lower molars, unusually wide talonids on the first and second lower molars, very well-developed conules on the upper molars, and a distinct distal protocone-fold. A

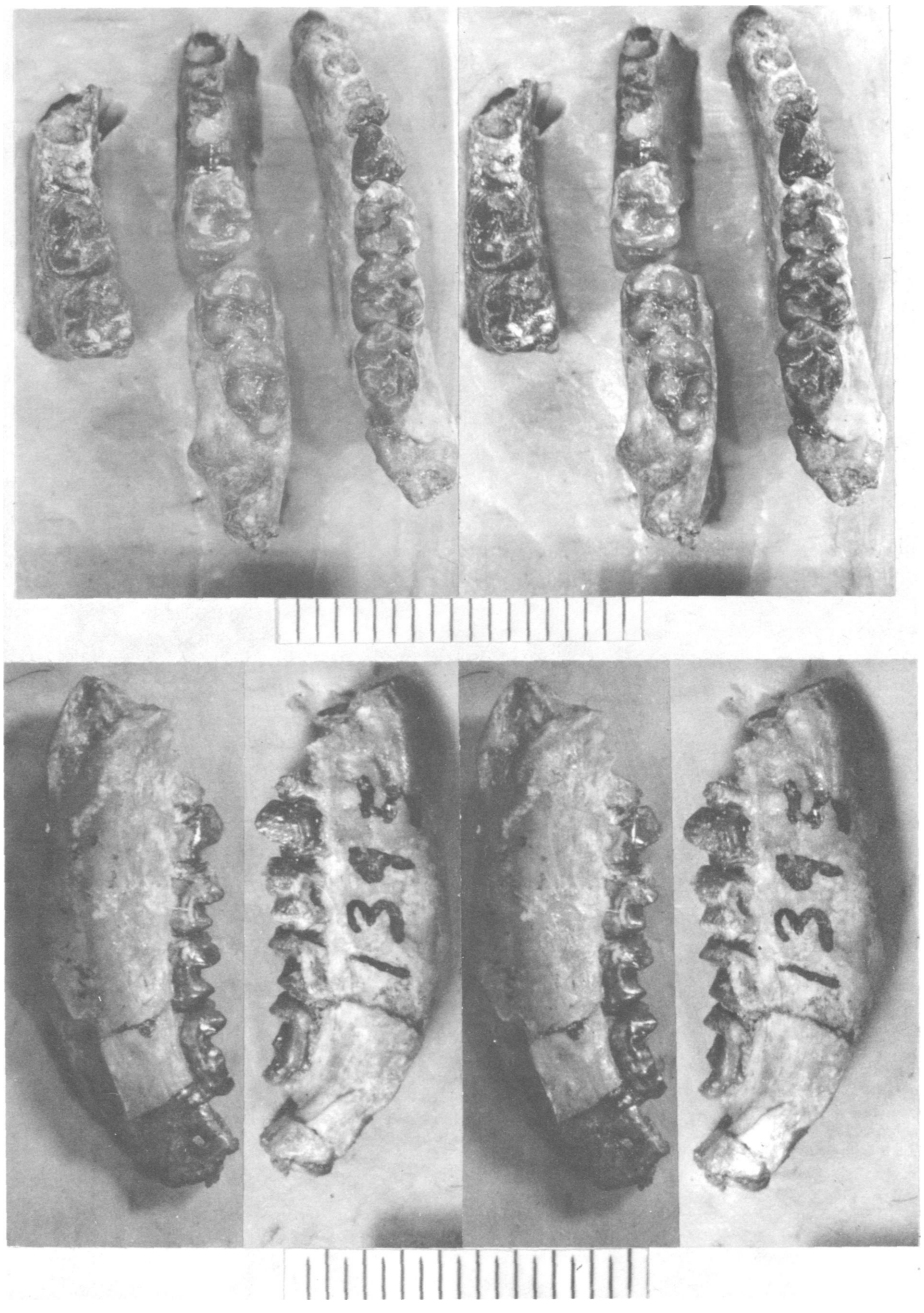


FIG. 101. *Dyseolemur pacificus*, LACM 1531, left M_{1-2} (above left); LACM 5195, left M_1 (above upper center); LACM 5192, left M_{2-3} (above lower center); LACM 1395, type, right P_3 (broken), P_4-M_3 (above right and below); all from Tapo Ranch, Sespe beds. Stereophotographs: above occlusal, below left medial, and below right lateral views. Subdivisions on scales represent 0.5 mm.

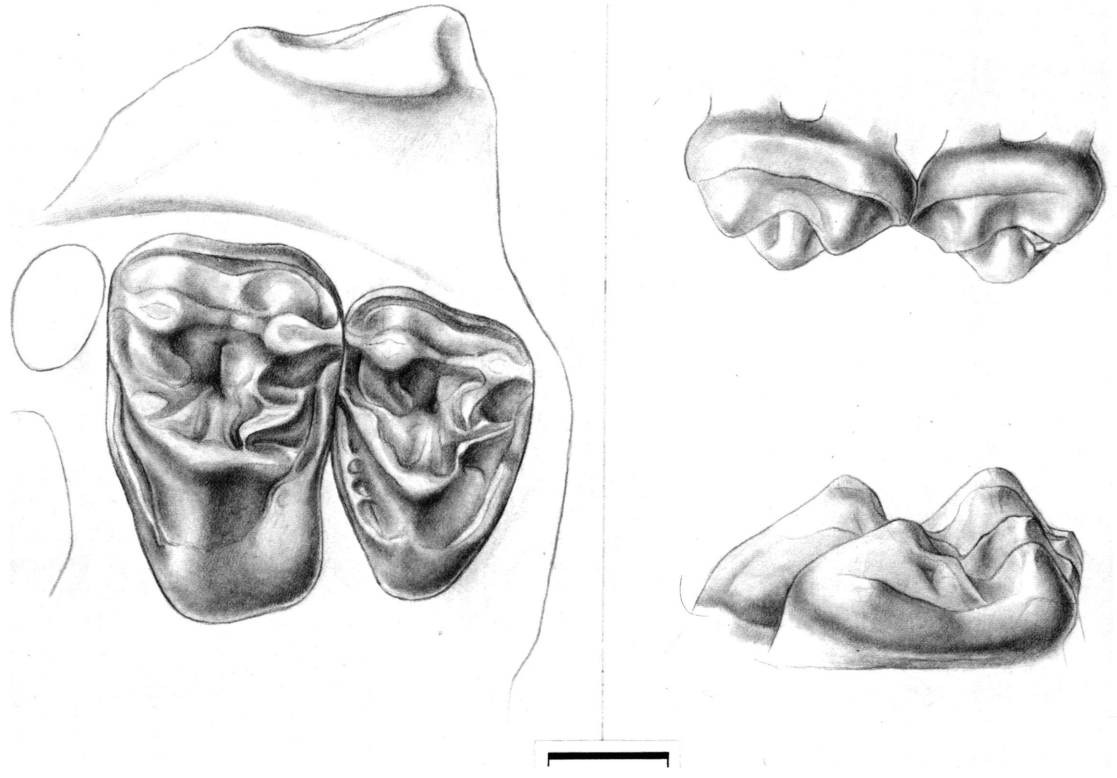


FIG. 102. *Dyseolemur pacificus*, left M^{2-3}, based on LACM 1520 and 1591, Uintan of California; occlusal (left), buccal (above right), and distal (below right) views. Scale represents 1 mm.

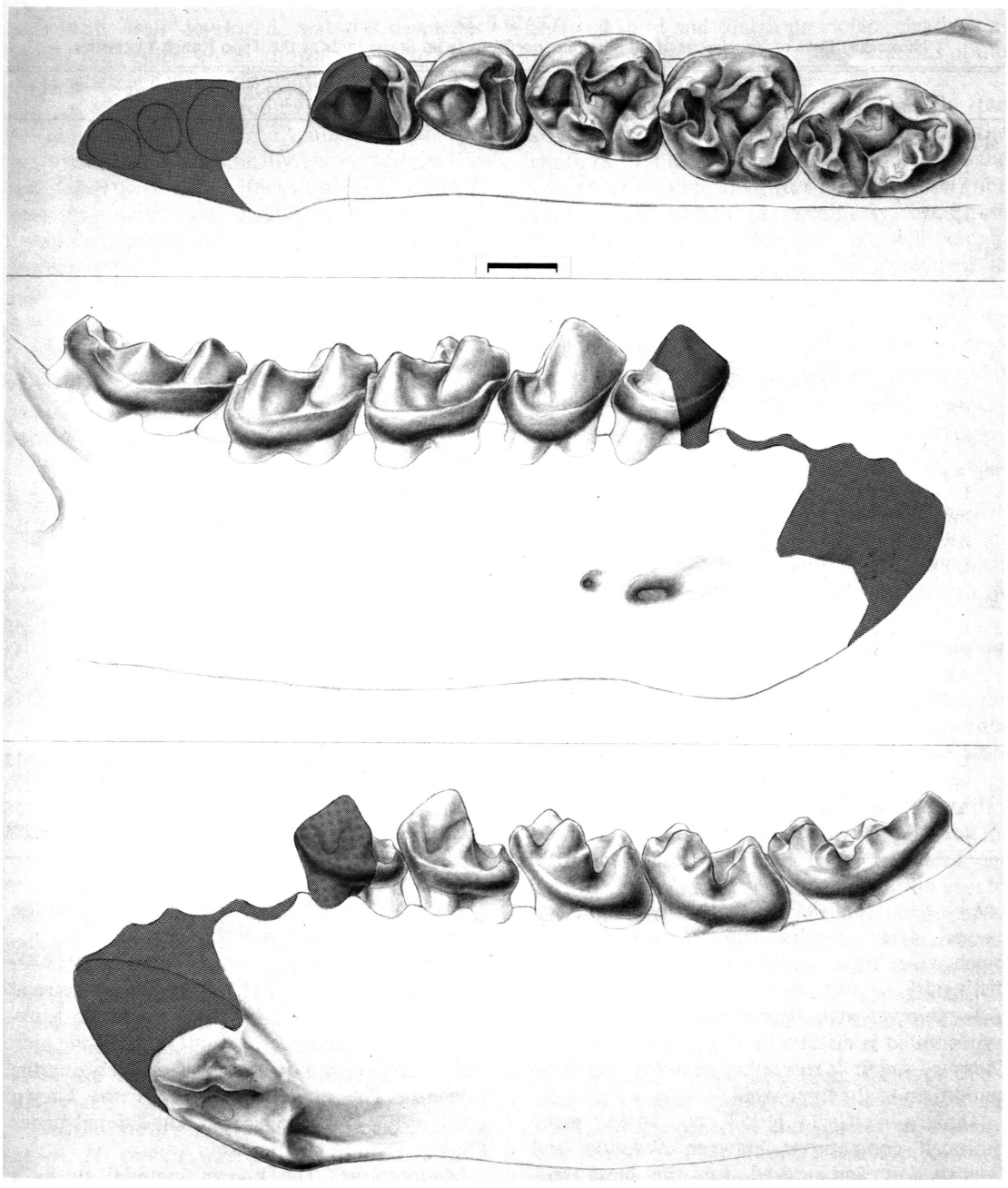


FIG. 103. *Dyseolemur pacificus*, right horizontal ramus with P_3-M_3, based on LACM 1395, type, Uintan of California; occlusal (above), lateral (middle), and medial (below) views. Reconstruction shown by uniform stippling. Scale represents 1 mm.

TABLE 22
Numerical Data of Specimens of *Dyseolemur pacificus* from Sespe Beds at the Tapo Ranch Localities

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
M^2								
L	2	1.90-1.92	–	–	–	–	–	–
AW	2	3.18-3.20	–	–	–	–	–	–
L/AW	2	0.60	–	–	–	–	–	–
M^3								
L	2	1.60-1.76	–	–	–	–	–	–
AW	2	2.51-2.60	–	–	–	–	–	–
L/AW	2	0.64-0.68	–	–	–	–	–	–
P_4								
L	2	1.64-1.65	–	–	–	–	–	–
PW	2	1.47-1.60	–	–	–	–	–	–
L/PW	2	1.02-1.12	–	–	–	–	–	–
M_1								
L	3	1.90-2.00	–	1.967±0.033	0.058±0.024	3.180±1.298	–	–
PW	3	1.70-1.89	0.967	1.810±0.057	0.098±0.040	5.895±2.407	–	–
AW	3	1.63-1.74	0.839	1.683±0.032	0.055±0.022	3.544±1.447	–	–
L/PW	3	1.06-1.12	–	1.088±0.017	0.030±0.012	2.961±1.209	–	–
M_2								
L	5	1.85-2.18	–	2.062±0.057	0.129±0.041	6.545±2.070	−1.473	2.245
PW	5	1.87-2.08	0.605	1.986±0.034	0.075±0.024	3.985±1.260	−0.706	2.043
AW	5	1.80-2.00	0.730	1.928±0.036	0.081±0.026	4.398±1.391	−1.245	0.947
L/PW	5	0.98-1.10	–	1.038±0.023	0.051±0.016	5.202±1.645	−0.117	−2.178
M_3								
L	4	2.45-2.70	–	2.617±0.057	0.114±0.040	4.645±1.642	−1.728	3.012
PW	4	1.50-1.72	0.953	1.655±0.053	0.105±0.037	6.743±2.384	−1.817	3.293
AW	4	1.50-1.78	0.906	1.670±0.062	0.124±0.044	7.878±2.785	−1.138	0.758
L/PW	4	1.53-1.63	–	1.583±0.021	0.042±0.015	2.787±0.985	0.101	−0.255

combination of the very heavily crenulated enamel, large conules, and talonids relatively much wider than trigonids (all derived features) distinguish *Hemiacodon* from other omomyines, *Ourayia* and *Macrotarsius* included. The hypoconulid is distinct in *Hemiacodon*, unlike in *Ourayia*, and it is somewhat nearer to the entoconid than to the hypoconid.

Discussion. Gazin (1958, pp. 54-55) made thorough comparisons between *Omomys* and *Hemiacodon* and argued for the close relationship of the latter to the former. He has, however, refrained from deriving *Hemiacodon gracilis*, the only known species of this genus, from either of the lower Bridger species of *Omomys*.

The known dental morphology is very distinct from any of the other omomyines, particularly omomyinines, and the most recent affinities appear to be possibly with *Loveina*.

Gazin (1958, p. 55) restated Simpson's (1940) conclusion, namely that the known postcranial anatomy appeared to be more similar to lemuroids than to tarsioids, without committing himself to a view for or against it or analyzing the evidence. The phyletic aspects of the known postcranials are discussed in some detail under Phylogeny and Classification.

Adaptations. The known material shows a number of highly derived character states which are very suggestive of mechanical adaptation for processing large amounts of vegetable foods. The hypocone is well developed, the conules are exceptionally large and rounded, the talonids relatively very broad, cingula and cingulids are ex-

ceptionally well developed, and the enamel is heavily crenulated on all known specimens. The lower anterior dentition is tightly packed and the anterior incisor is very robust. The jaw tends to be deep and robust and the symphysis, although not synostosed, occasionally shows very extensive rugosity (see fig. 109) in older specimens, suggesting symphyseal rigidity while masticating.

All the specializations point to increasing the mechanical efficiency for some form of a phytophagous diet.

Hemiacodon gracilis Marsh, 1872
Figures 104-111; Table 23

Hemiacodon gracilis Marsh, 1872, p. 212.
Omomys gracilis Osborn, 1902, p. 173.

Type. YPM 11806, right mandible fragment with P_3-M_3; collected from Bridger C or D beds, at Henry's Fork, Bridger Basin, Wyoming.

Hypodigm. The type and AMNH 12012, 12018, 12019, 12023, 12024, 12027, 12029, 12030, 12033, 12059, 12608, 12609, 12611, and 18991; YPM 11806, 12013, and 12014, and numerous others; all of the hypodigm is from Bridger beds C or D, above the Sage Creek white layer.

Geographical and Temporal Distribution. Same as for the genus.

Specific Diagnosis. Only known species of the genus.

Dental Formula. $I\frac{1,2}{1,2}; C\frac{1}{1}; P\frac{2,3,4}{2,3,4}; M\frac{1,2,3}{1,2,3}$.

Discussion. This is one of the best known species of the Omomyidae. Dozens of mandible and maxilla fragments are known and a frontal fragment (USNM 21878) has been described by Gazin (1958, p. 55). Postcranial remains allocated to *H. gracilis* have been described and discussed by Simpson (1940) and some aspects of them are further evaluated below under Phylogeny and Classification.

Judged from the cranial and postcranial remains, *H. gracilis* was the size of *Tarsius spectrum* or slightly larger.

TRIBE UINTANIINI, NEW

Type Genus. Uintanius Matthew, 1915.
Included Genera. Type genus only.
Tribe Diagnosis. Omomyines with greatly enlarged third and fourth premolars, clearly convergent, however, to similar specializations of the anaptomorphine *Absarokius.*

Discussion. To express taxonomically the striking specializations of this genus within the confines of the Omomyinae, and to balance the taxonomy within the whole family, the tribe Uintaniini is established. It is likely that future discoveries of new omomyid taxa will contain species which will be unequivocally referred to this tribe. This new tribe helps to show taxonomically the convergence of *Uintanius* to the paromomyid *Micromomys* and *Tinimomys*, and the tetoniinan anaptomorphine *Absarokius* among early Tertiary primates.

UINTANIUS MATTHEW, 1915

Omomys: Wortman, 1904, p. 134.
Uintanius Matthew, 1915, p. 455.
Huerfanius Robinson, 1966, p. 35.

Type Species. Uintanius ameghini (Wortman, 1904).

Included Species. The type species and *Uintanius vespertinus.*

Geographical and Temporal Distribution. Wasatchian to early Bridgerian (early to medial Eocene) of New Mexico and Wyoming, and Colorado, respectively.

Generic Diagnosis. Omomyines that differ from all other taxa of the subfamily in having the paracones and protoconids of the third and fourth premolars enlarged greatly in the genero-type and to a lesser degree in the referred species. Paraconid on M_1 of the latter is characteristically more mesial than in other omomyines. Presence of the protocone-fold distinguishes the upper molars of *Uintanius* from those of *Chumashius* and *Omomys.*

Discussion. When describing the type specimen of *Uintanius ameghini*, Wortman (1904, p. 134) astutely referred the species to *Omomys* and not to the then known anaptomorphines. In 1958, when reviewing *Uintanius*, Gazin referred the genus to the Anaptomorphinae, as did Simpson in 1940 and 1945 and derived it from the vicinity of *Absarokius*. This view on *Uintanius* persisted as Simons (1963); McKenna (1967); and Russell, Louis, and Savage (1967) continued to list this genus as an anaptomorphine. In 1966

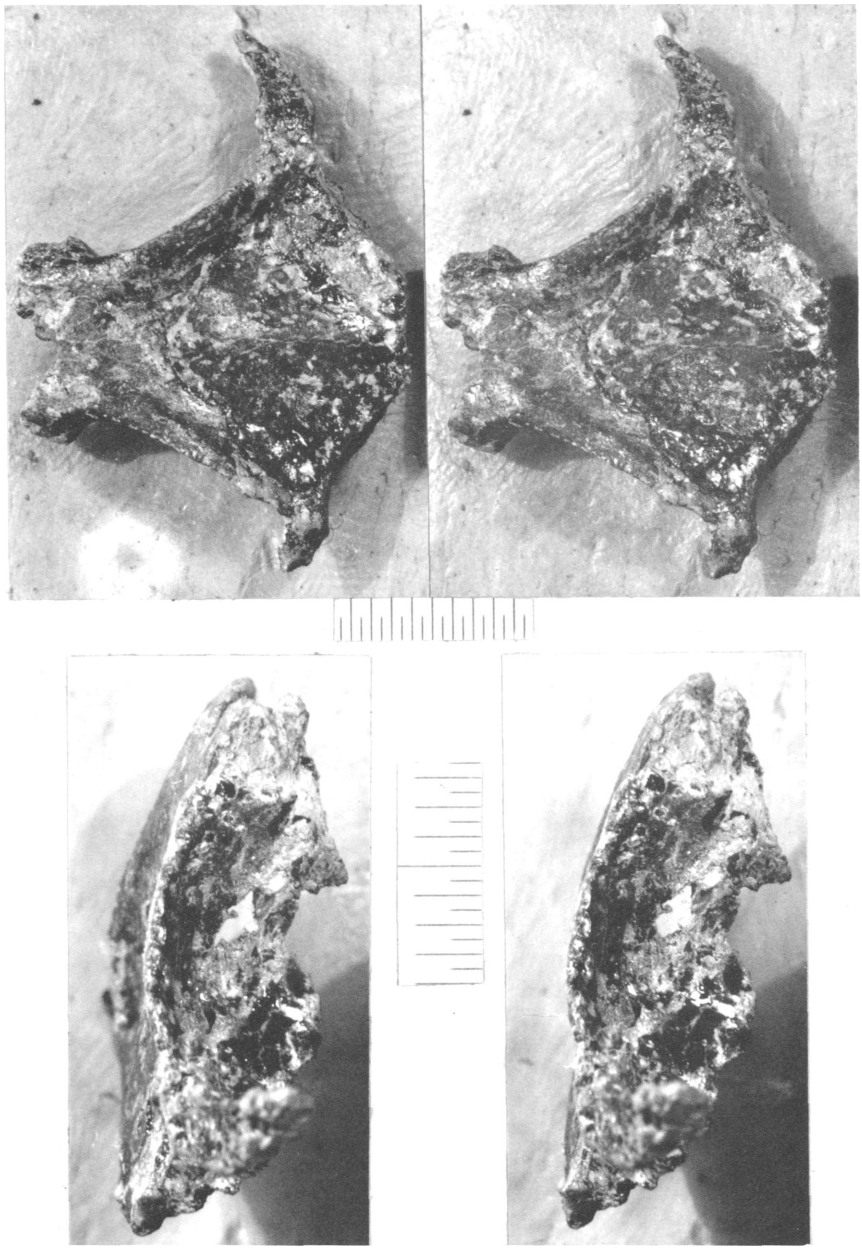


FIG. 104. *Hemiacodon gracilis*, USNM 21878, Bridger beds, frontal fragment. Stereophotographs: above dorsal (front to the left) and below lateral views (front toward the top). Subdivisions on scales represent 0.5 mm.

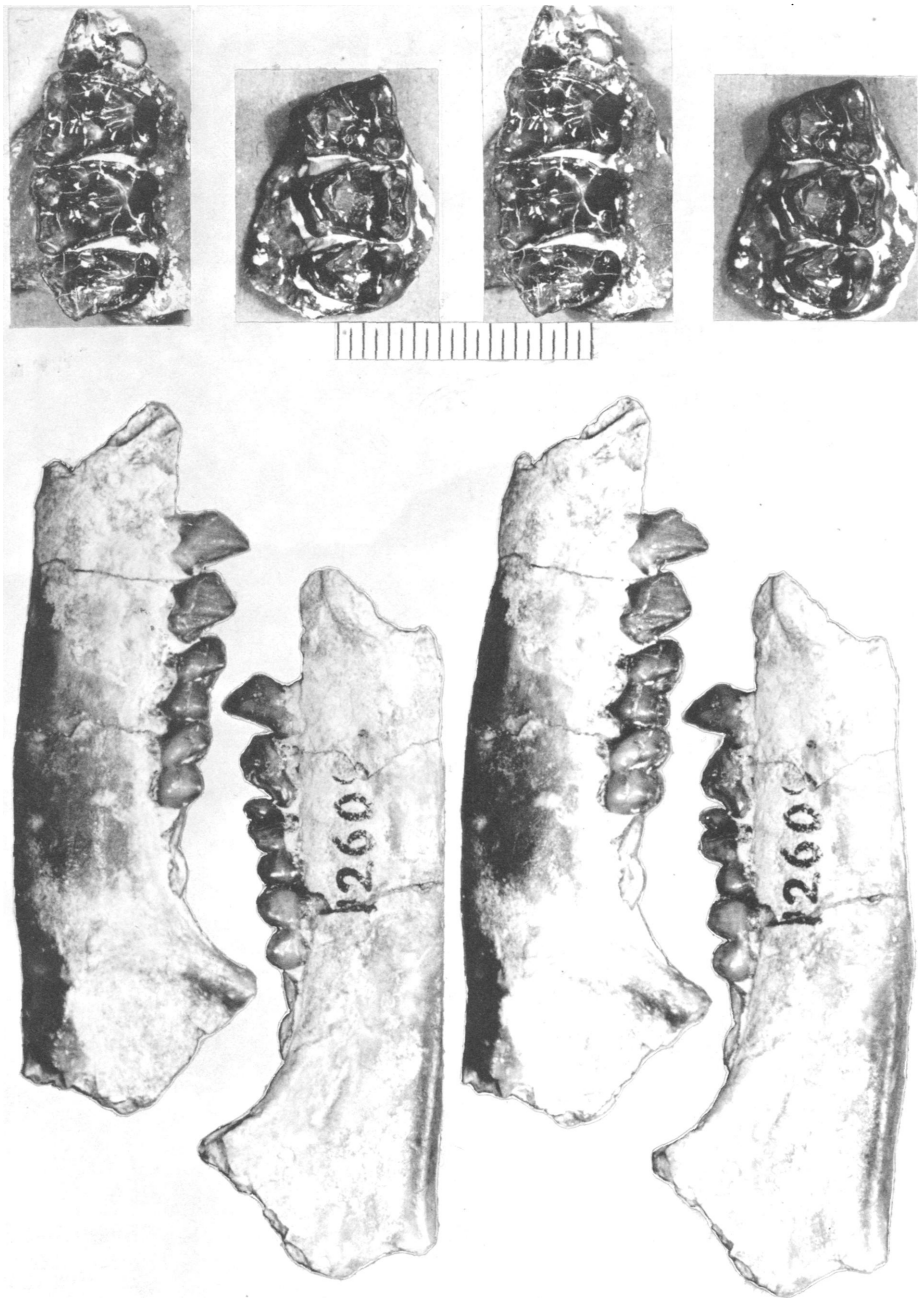


FIG. 105. *Hemiacodon gracilis*, AMNH 12030, right M^{1-3} (above left); AMNH 12018, left M^{1-3} (above right); AMNH 12609, left P_3-M_2 (below); all from Bridger beds. Stereophotographs: above occlusal, below left lateral, below right medial views. Subdivisions on scale represent 0.5 mm.

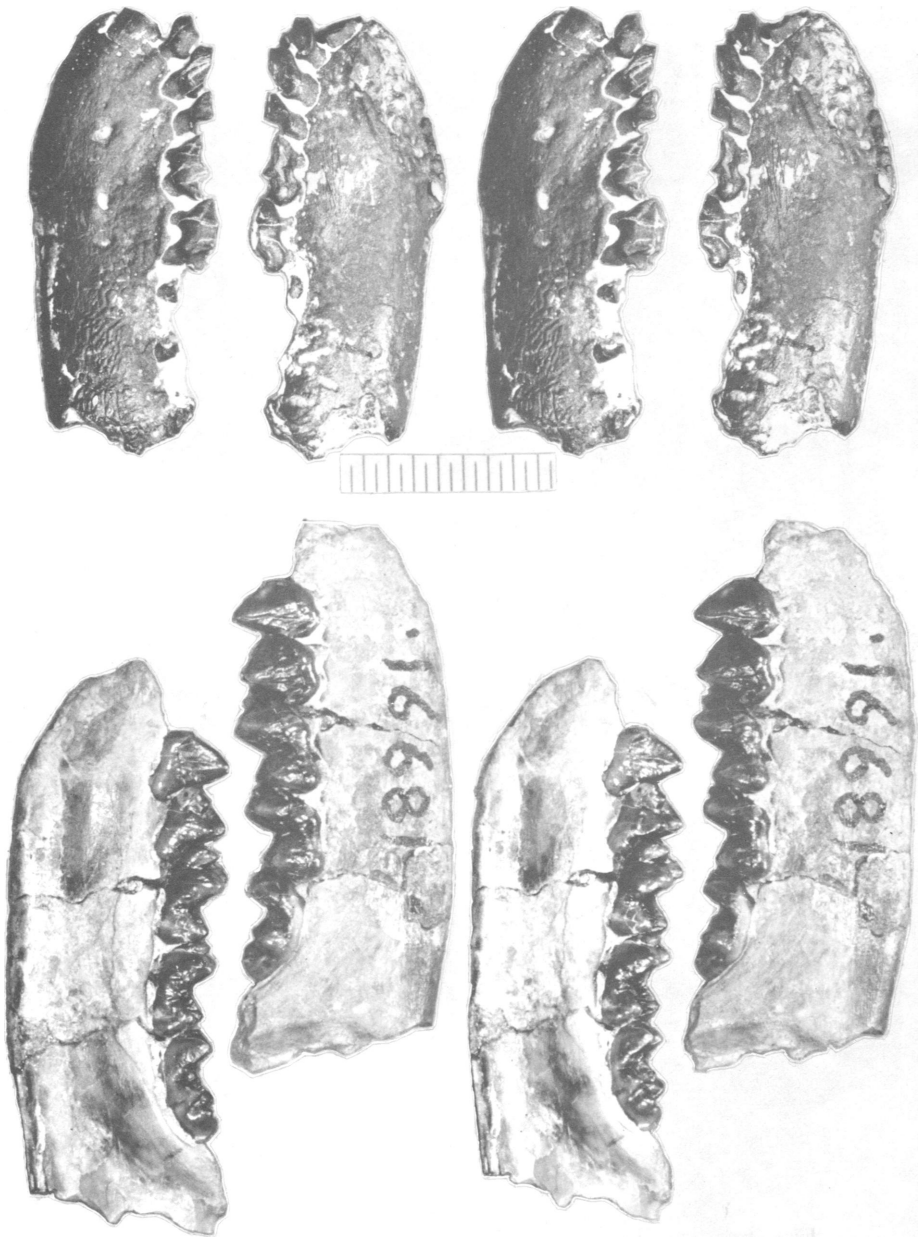


FIG. 106. *Hemiacodon gracilis*, AMNH 12037, left I_2-P_4 (above) and AMNH 18991, right P_3-M_3 (below), both from Bridger beds. Stereophotographs: above left lateral, above right medial, below left lateral, below right medial views. Subdivisions on scale represent 0.5 mm. Scale pertains to AMNH 12037.

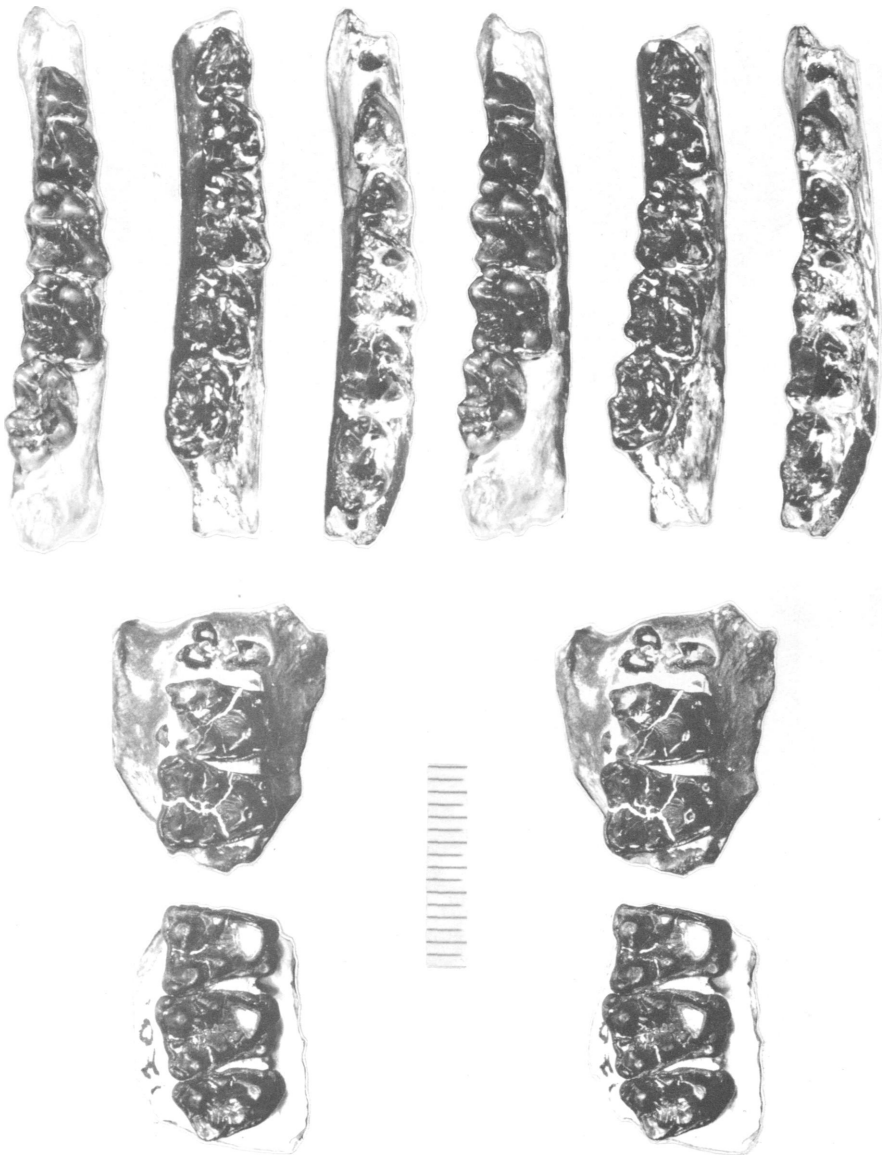


FIG. 107. *Hemiacodon gracilis*, AMNH 18991, right P_4-M_3 (above left); AMNH 12609, right P_4-M_3 (above middle); AMNH 11806, right P_4-M_3 (above right); AMNH 12029, left M^{1-2} (middle); and AMNH 12012, right M^{1-3} (below); all from Bridger beds. Stereophotographs: all occlusal views. Subdivisions on scale represent 0.5 mm.

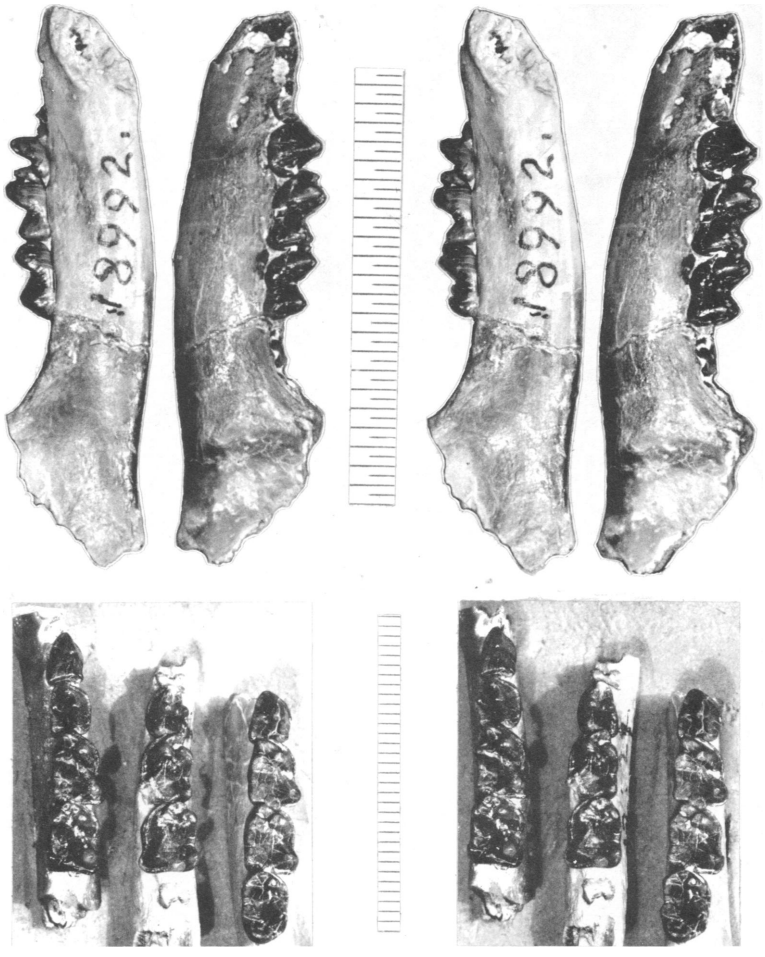


FIG. 108. *Hemiacodon gracilis*, AMNH 18992, left P_4-M_2 (above); AMNH 12027, right P_3-M_2 (below left); AMNH 12021, left P_4-M_2 (below center); AMNH 12021, right P_4-M_3 (below right); all from Bridger beds. Stereophotographs: above left medial, above right lateral, below occlusal views. Subdivisions on scale represent 0.5 mm.

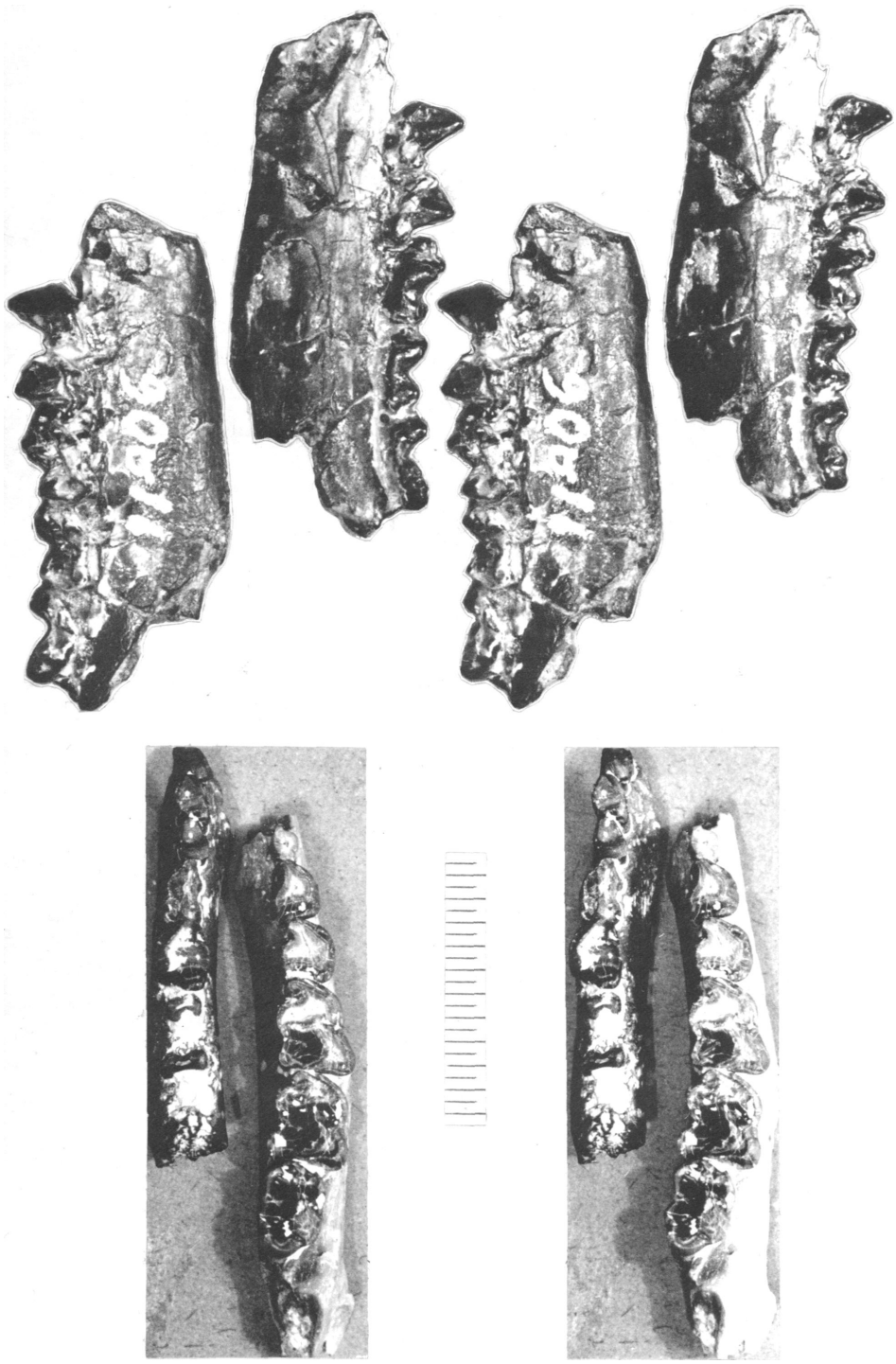


FIG. 109. *Hemiacodon gracilis*, YPM 11806, type, right P_3-M_3 (above); AMNH 12037, left I_1-P_4 (below left); and AMNH 12014, right P_3-M_3 (below right); all from Bridger beds. Stereophotographs: above left lateral, above right medial, below occlusal views. Subdivisions on scale represent 0.5 mm.

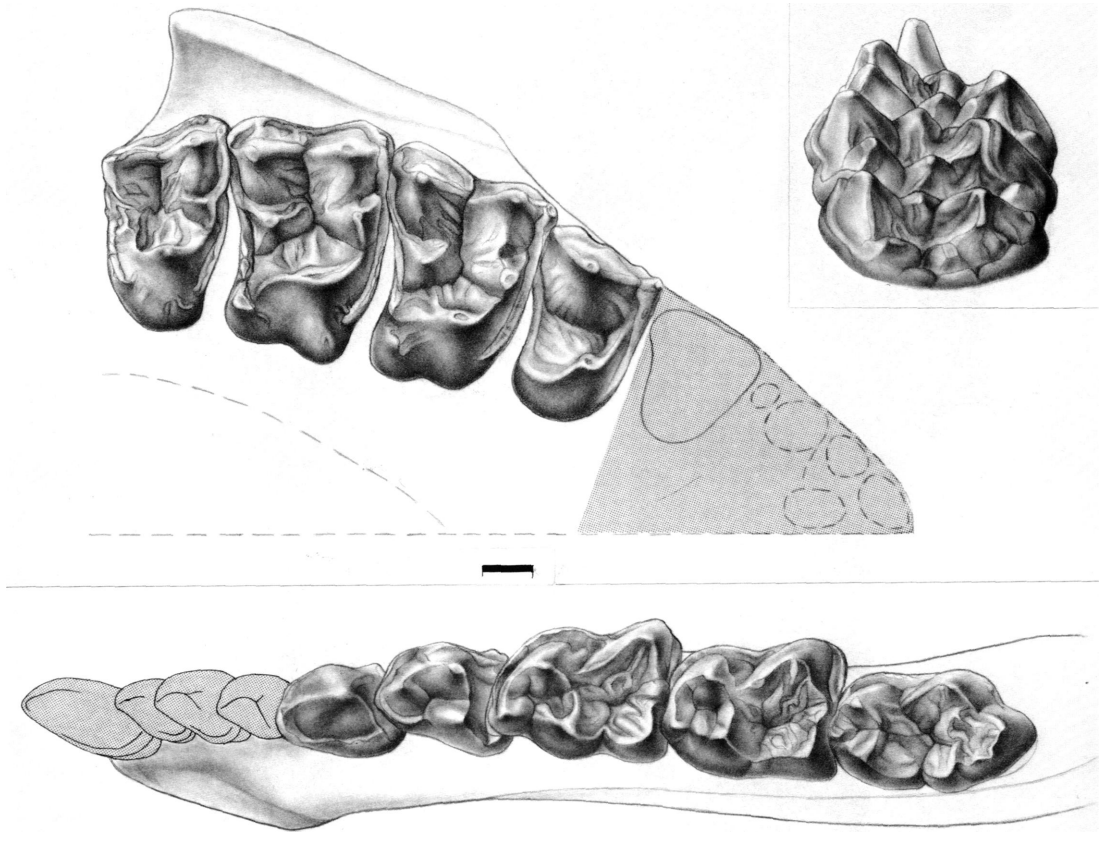


FIG. 110. *Hemiacodon gracilis*, right P^4-M^3 (above), based on AMNH 12030, left P_3-M_3 (below), based on AMNH 12037 and 18991, Bridgerian of Wyoming; above left and below occlusal and upper right corner occlusodistal views, respectively. Reconstruction shown by uniform stippling and broken lines. Scale represents 1 mm.

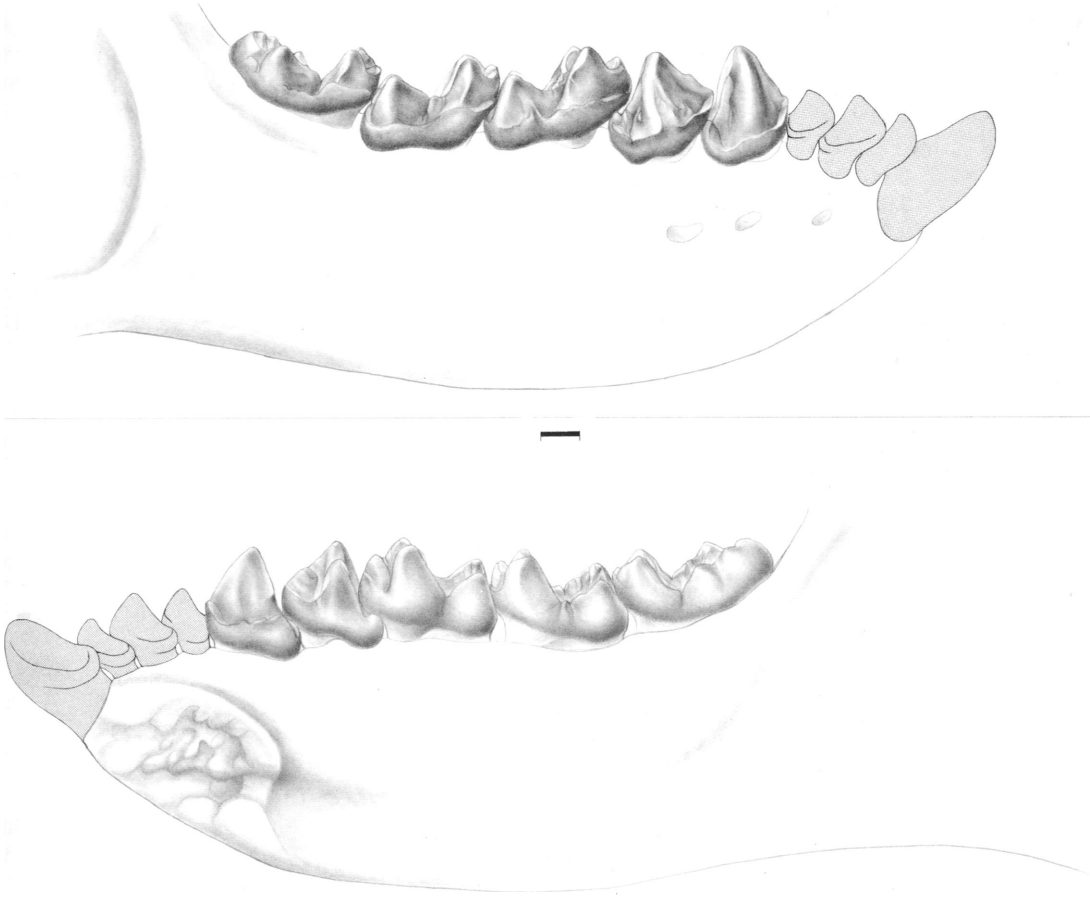


FIG. 111. *Hemiacodon gracilis*, left mandible with dentition (I_1-M_3), based on AMNH 12037, 18991, and 18992, Bridgerian of Wyoming; lateral (above) and medial (below) views. Reconstruction shown by uniform stippling. Scale represents 1 mm.

TABLE 23
Numerical Data for Specimens of *Hemiacodon gracilis* Presumably All from Upper (C and D) Bridger Beds

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
M^1								
L	5	3.39-3.70	–	3.598±0.062	0.139±0.044	4.046±1.279	−1.063	−0.656
AW	5	4.27-4.80	0.823	4.518±0.098	0.220±0.070	5.114±1.617	0.020	−1.744
L/AW	5	0.77-0.82	–	0.797±0.010	0.022±0.007	2.892±0.915	−0.309	−0.291
M^2								
L	6	3.18-3.51	–	3.382±0.046	0.112±0.032	3.449±0.996	−1.234	2.423
AW	6	4.65-5.00	0.208	4.852±0.050	0.123±0.035	2.631±0.760	−0.672	0.700
L/AW	6	0.66-0.73	–	0.697±0.011	0.026±0.008	3.932±1.135	0.130	−1.276
M^3								
L	4	2.55-2.90	–	2.782±0.079	0.158±0.056	6.025±2.130	−1.788	3.385
AW	4	3.88-4.30	0.960	4.145±0.094	0.187±0.066	4.802±1.698	−1.392	1.733
L/AW	4	0.66-0.69	–	0.671±0.006	0.013±0.004	1.994±0.705	0.366	−0.501
P_3								
L	7	2.60-3.05	–	2.796±0.053	0.140±0.037	5.190±1.387	0.691	1.559
PW	7	1.89-2.20	0.484	2.007±0.046	0.121±0.032	6.240±1.668	0.794	−0.877
L/PW	7	1.29-1.50	–	1.395±0.030	0.079±0.021	5.874±1.570	−0.371	−1.021
P_4								
L	12	2.80-3.15	–	2.982±0.028	0.096±0.020	3.280±0.670	0.000	0.407
PW	12	2.08-2.40	0.367	2.203±0.025	0.087±0.018	4.031±0.823	0.852	1.204
L/PW	12	1.24-1.42	–	1.355±0.016	0.054±0.011	4.103±0.838	−0.967	0.101
M_1								
L	14	3.29-3.94	–	3.628±0.045	0.169±0.032	4.755±0.899	−0.246	0.174
PW	14	2.70-3.33	0.522	2.881±0.041	0.154±0.029	5.446±1.029	1.965	5.410
AW	14	2.50-2.96	0.610	2.653±0.033	0.125±0.024	4.786±0.904	1.169	1.363
L/PW	14	1.18-1.34	–	1.261±0.017	0.062±0.012	5.002±0.945	0.041	−1.645
M_2								
L	16	3.10-3.80	–	3.534±0.048	0.192±0.034	5.523±0.976	−1.050	0.570
PW	16	2.70-3.35	0.629	2.924±0.038	0.151±0.027	5.234±0.925	1.456	3.579
AW	16	2.57-3.10	0.494	2.816±0.032	0.128±0.023	4.624±0.817	0.129	1.212
L/PW	16	1.10-1.28	–	1.210±0.014	0.055±0.010	4.618±0.816	−0.249	−0.723
M_3								
L	9	3.57-4.55	–	4.093±0.096	0.287±0.068	7.212±1.700	−0.457	0.460
PW	9	2.13-2.70	0.838	2.469±0.061	0.183±0.043	7.612±1.794	−0.745	0.021
AW	9	2.10-2.63	0.714	2.438±0.059	0.178±0.042	7.509±1.770	−0.776	0.019
L/PW	9	1.55-1.74	–	1.660±0.022	0.067±0.016	4.123±0.972	−0.431	−0.763

Robinson described a new genus from the Huerfano Formation, called "*Huerfanius*," based on a new species, "*H. rutherfurdi*." He compared the species to anaptomorphines and to *Uintanius ameghini* which he considered as an anaptomorphine. He failed to describe a single diagnostic feature that would differentiate "*Huerfanius*" from *Uintanius*, primarily because he, as well as Gazin (1958), overlooked the fact that the third and fourth premolars in AMNH 12598 are deciduous and not permanent. "*Huerfanius*" is represented on the phylogenetic chart of Russell, Louis, and Savage (1967), but no line, indicating a path of descent, is shown between *Uintanius* and the Huerfano taxon.

Uintanius is much more similar to *Loveina*,

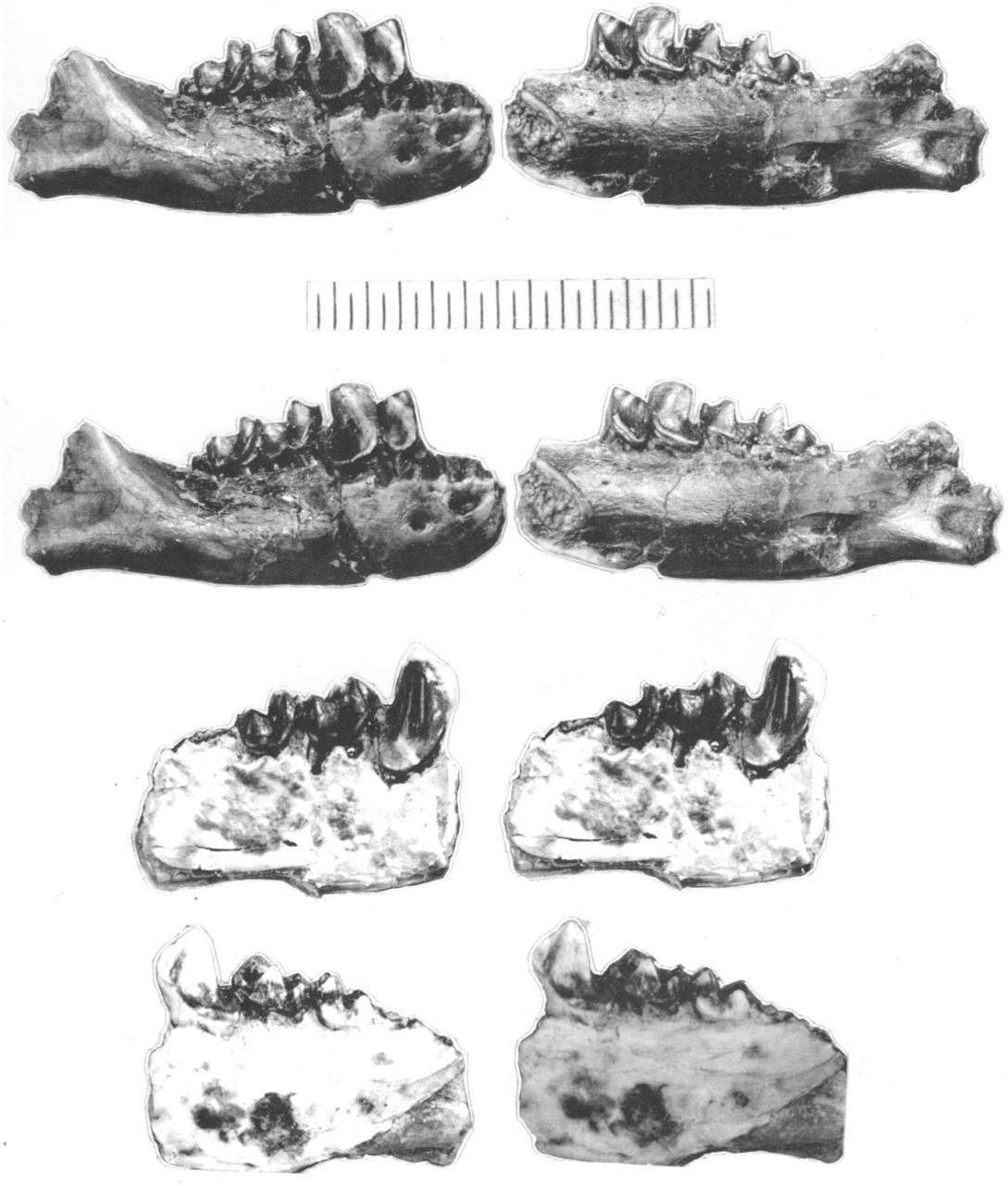


FIG. 112. *Uintanius ameghini*, AMNH 12598, type of "*Uintanius turriculorum*," right dP_3, dP_4, M_{1-2} (above) and UW 1566, right P_4-M_2 (below), both from Bridger beds. Stereophotographs: above left and below top lateral and above right and below bottom medial views. Subdivisions on scale represent 0.5 mm.

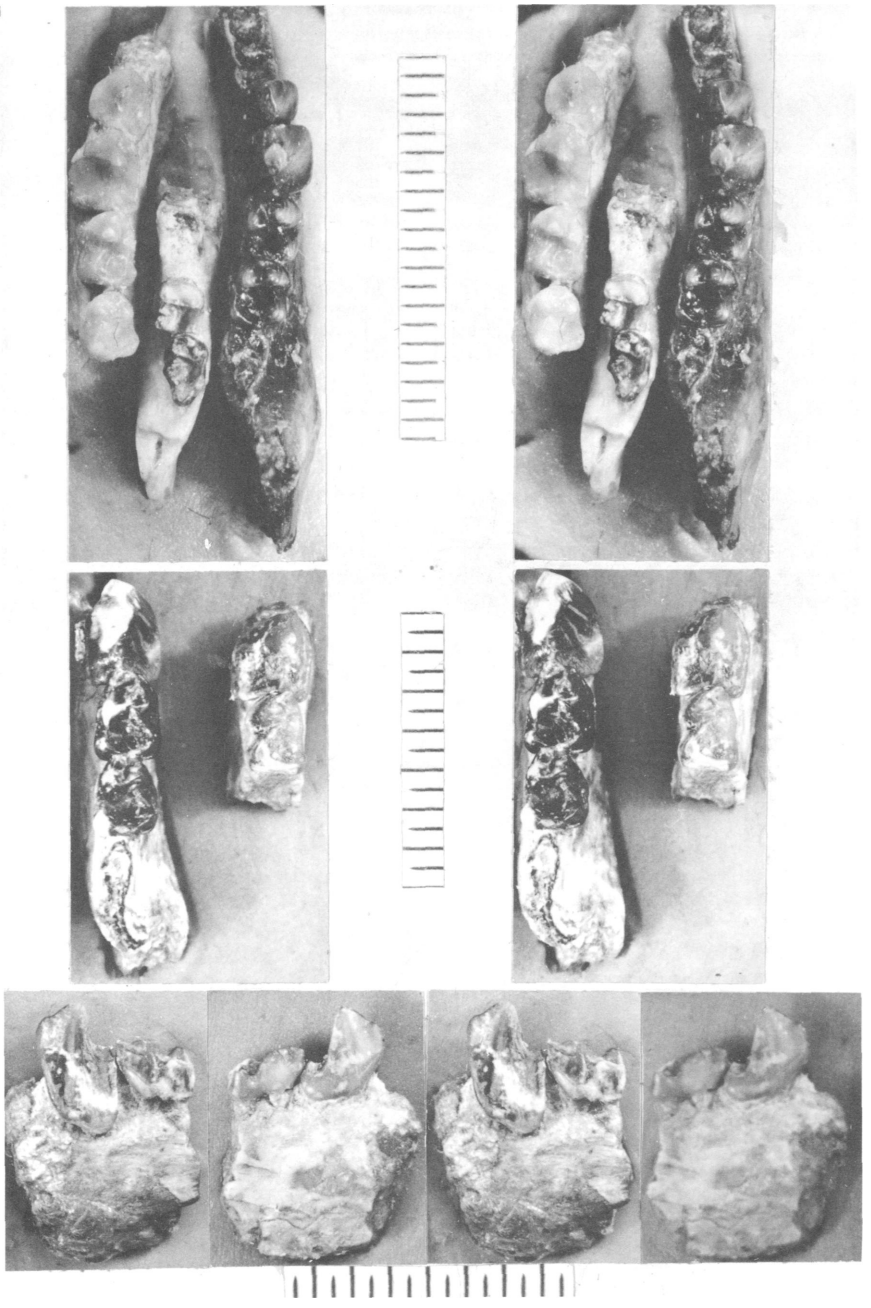


FIG. 113. *Uintanius ameghini*, AMNH 55216, type of "*Huerfanius rutherfurdi*," Huerfano beds, left P_3-M_2 (above left); YPM 13241, type, Bridger beds, left M_{2-3} (above center); AMNH 12598, type of "*Uintanius turriculorum*," Bridger beds, left dP_3, dP_4, M_{1-2} (above right); UW 1566, Big Sandy, Bridger beds, right P_4-M_2 (middle left); and UC 26533, Huerfano loc. III, left P_4-M_1 (middle right and below). Stereophotographs: above and middle occlusal, below left lateral and below right medial views. Subdivisions on scales represent 0.5 mm.

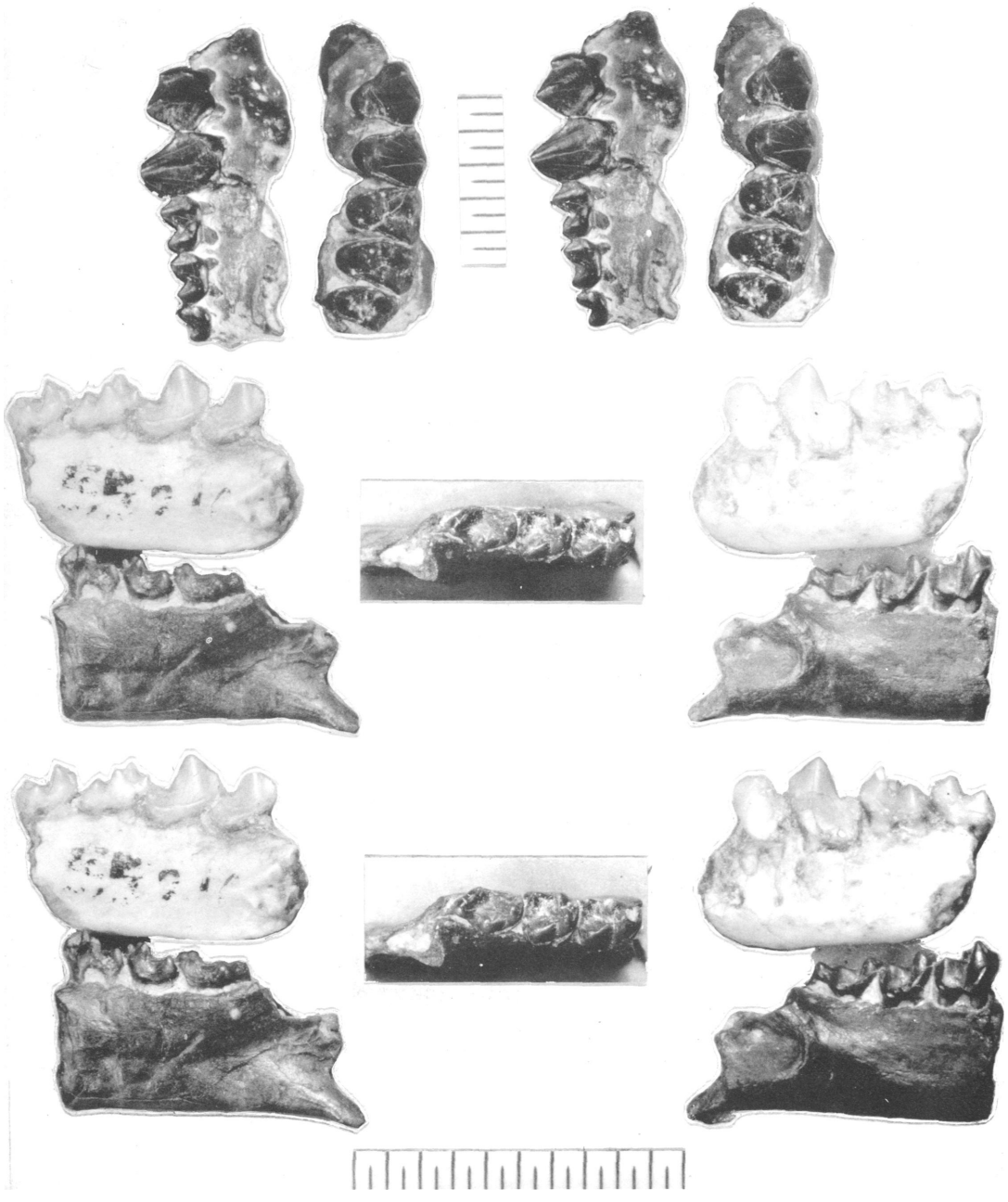


FIG. 114. *Uintanius ameghini*, AMNH 13039, Bridger beds, left P^3-M^3 (above); AMNH 55216, type of "*Huerfanius rutherfurdi*," loc. II, Huerfano beds, left P_3-M_2 (second and fourth rows, left and right); and AMNH 12376, Bridger Formation, right M_{1-3} (third and fifth rows, left and right, and center). Stereophotographs: above left, lateral, above right and center occlusal, below left, medial, and below right, lateral views. Subdivisions on scales represent 0.5 mm.

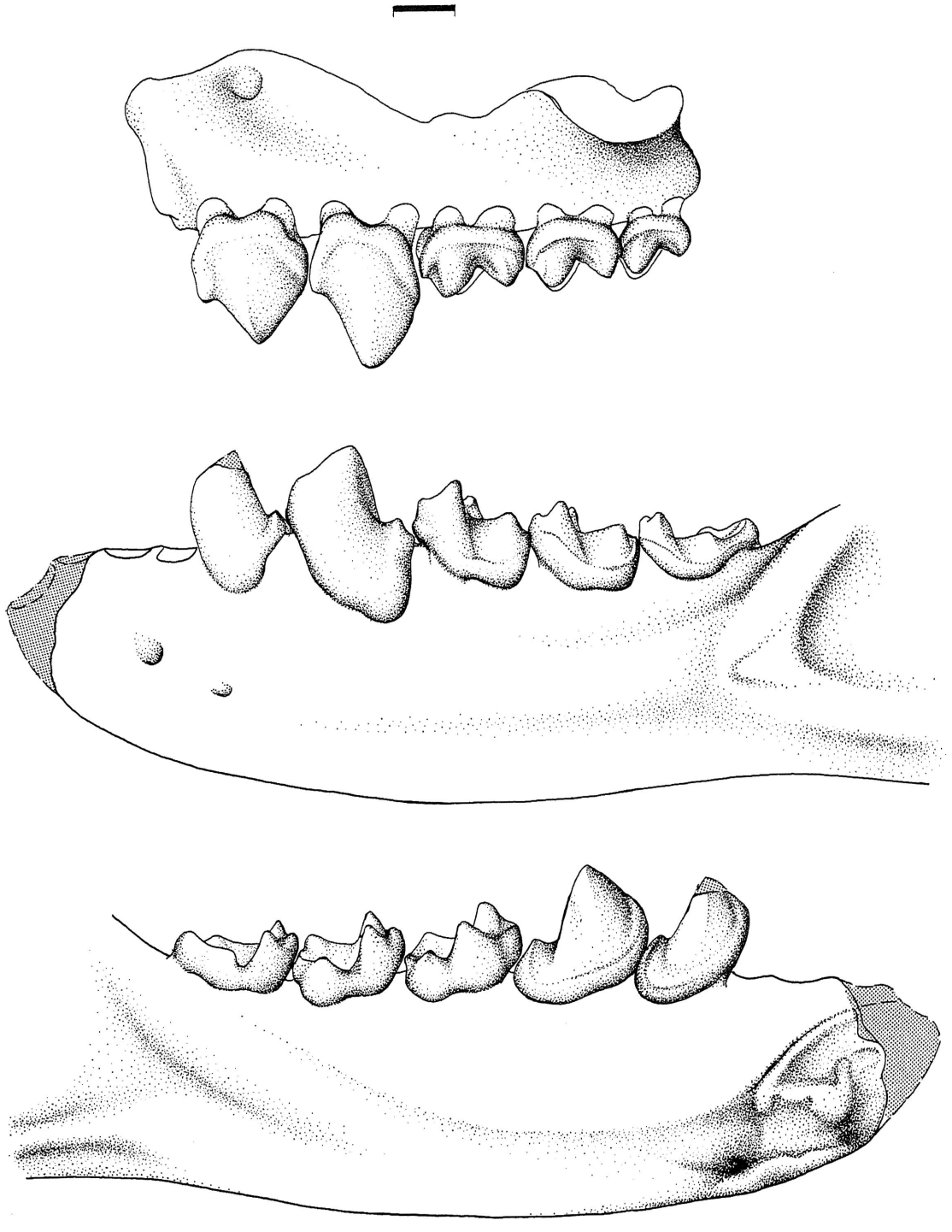


FIG. 115. *Uintanius ameghini*, left P^3-M^3 (above), based on AMNH 13039, and left horizontal ramus with P_3-M_3 (below), based on AMNH 12598, type of "*Uintanius turriculorum*," and AMNH 55216 and 12376, Bridgerian of Wyoming and Colorado; lateral (above and middle) and medial (below) views, respectively. Reconstruction shown by uniform stippling and by broken lines. Scale represents 1 mm.

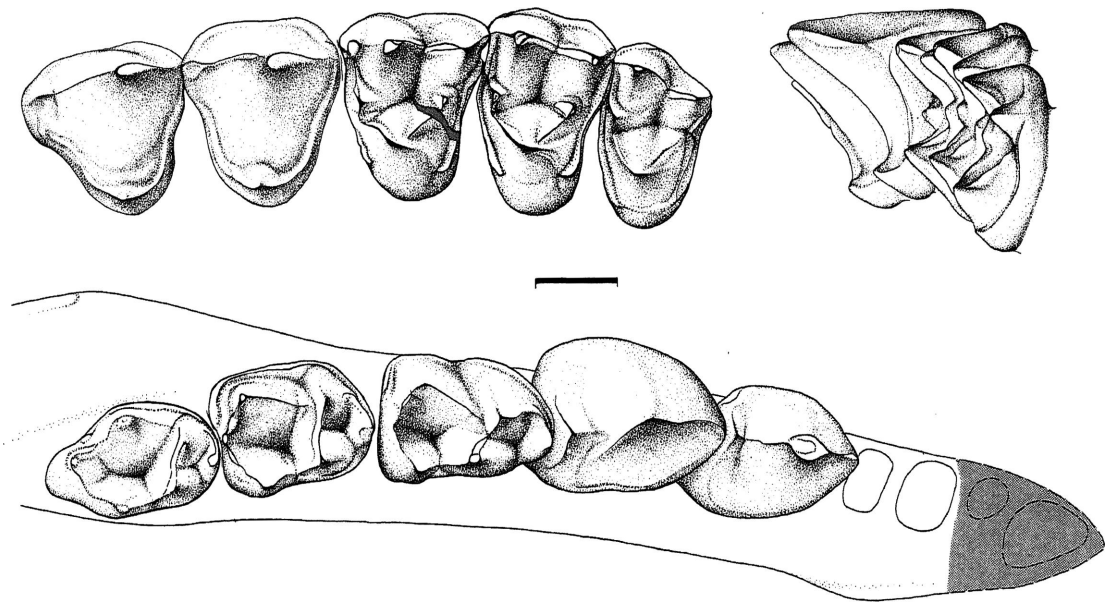


FIG. 116. *Uintanius ameghini*, left P^3-M^3 and left P_3-M_3, based on AMNH 13039, 56216, 12376, and 55216, Bridgerian of Wyoming and Colorado; occlusal (above left and below) and occlusodistal (above right) views. Reconstruction shown by uniform stippling and broken lines. Scale represents 1 mm.

Omomys, and *Chumashius* than to any of the Anaptomorphinae. The trigonid cusps lack the inflated base characteristic of the latter group, and the last molars are not much smaller than the more anterior ones. The morphology of the M_3 talonid is very similar to that found in the omomyines cited. It is possible that all of the noted similarities to omomyines represent primitive omomyid characters and genealogically *Uintanius* has more recently shared a common ancestor with some unknown anaptomorphine, but I doubt this. Furthermore, the derived character states of the third and fourth premolars are not homologous with those of *Absarokius*, which is the previously implied base for considering *Uintanius* an anaptomorphine. Modifications of the premolars in the two genera are almost certainly convergent.

Adaptations. This assessment of adaptations refers to the type species *U. ameghini* although the characters of the latter are present in at least an incipient form in *U. vespertinus*.

Obviously the most derived adaptations of *Uintanius* lie in the great vertical and mesiodistal enlargement of the paracones and protoconids of the third and fourth premolars. The relatively transverse upper molars are not very broad lingually, a protocone fold is well developed, but a true hypocone is absent. Neither upper nor lower last molars are reduced. The trigonids are relatively large and that of M_1 is very derived in that it is mesiodistally stretched out, clearly supplementing the extensive cutting edges of the premolars running in that direction.

Among modern forms, particularly in *Phaner*, and to some degree in *Euoticus* and *Perodicticus*, there is excessive enlargement of one premolar behind a very large upper canine and large caniniform P_2. In *Phaner* this has been correlated with gum and resin feeding habits (Petter, Schilling, and Pariente, 1971), as the teeth and the hypertrophied tooth comb and upper incisors are used to scrape bark to get at these nutrients. In *Uintanius* the enlarged teeth are probably too far back in the mouth for a similar biological role.

It is very difficult to judge the specialized adaptations in the tiny *Uintanius*. Because the emphasis is not on the canine or the incisors but on the posterior premolars one may suggest at first that food preparation (i.e., mastication in a

broad sense) rather than procurement or killing was the likely selective factor. The adaptations, however, are greatly accentuated shear in a limited area on the tooth row, namely the buccal side of the premolars. This could signify specializations for a particular type of plant material which required either tearing off as the material was placed in the mouth, or opening, slashing of succulent fruits or seed pods which required great force for penetration but no particular need to continually triturate to process for consumption. I consider the specialized premolars and the characteristic molar morphology to represent adaptations for some sort of insectivory and frugivory.

Uintanius ameghini (Wortman, 1904)
Figures 112-116; Table 24

Omomys ameghini Wortman, 1904, p. 134.
Uintanius turriculorum Matthew, 1915, p. 456.
Huerfanius rutherfurdi Robinson, 1966, p. 35.

Type. YPM 13241, left mandible fragment with M_{2-3}; collected from Bridger beds, Bridger Basin, Wyoming.

Hypodigm. The type, and AMNH 13039, the latter from Bridger "C"; AMNH 12376, collected from Bridger D; AMNH 12598, collected from lower Bridger beds (B) at Grizzly Buttes, Bridger beds; UW 1566, 2985, 3032, collected from Bridger A beds; AMNH 55216 and UC 26533, locs. II and III, respectively, upper faunal zone, Huerfano Formation, Colorado.

Geographical and Temporal Distribution. Early Bridgerian (early medial Eocene) of Wyoming and Colorado.

Specific Diagnosis. Differs from *U. vespertinus* in the more enlarged state of the third and fourth premolars and in having a more mesially placed paraconid on M_1.

Dental Formula. $I\frac{1,2}{1,2}$; $C\frac{1}{1}$; $P\frac{2,3,4}{2,3,4}$; $M\frac{1,2,3}{1,2,3}$.

Discussion. AMNH 12598, a mandible with dP_{3-4} and M_{1-2}, is the type specimen of "*Uintanius turriculorum*." The specimen is slightly damaged in that the premolars are artificially twisted posteriorly. A remarkable feature of this specimen, not noticed before, is the relatively much

TABLE 24
Numerical Data of *Uintanius* spp. from Various Bridger Localities and the Big Sandy Fauna (This sample probably contains more than one species.)

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P^3								
L	1	1.85	–	–	–	–	–	–
AW	1	1.95	–	–	–	–	–	–
L/AW	1	0.95	–	–	–	–	–	–
P^4								
L	1	1.75	–	–	–	–	–	–
AW	1	2.00	–	–	–	–	–	–
L/AW	1	0.88	–	–	–	–	–	–
M^1								
L	1	1.65	–	–	–	–	–	–
AW	1	2.10	–	–	–	–	–	–
L/AW	1	0.79	–	–	–	–	–	–
M^2								
L	1	1.50	–	–	–	–	–	–
AW	1	2.25	–	–	–	–	–	–
L/AW	1	0.67	–	–	–	–	–	–
M^3								
L	1	1.15	–	–	–	–	–	–
AW	1	1.90	–	–	–	–	–	–
L/AW	1	0.61	–	–	–	–	–	–

TABLE 24–(*Continued*)

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P_3								
L	2	1.60-1.70	–	–	–	–	–	–
PW	2	1.70-2.00	–	–	–	–	–	–
L/PW	2	0.80-1.00	–	–	–	–	–	–
P_4								
L	4	2.00-2.40	–	2.212±0.083	0.165±0.058	7.933±2.805	−0.437	1.166
PW	4	1.90-2.30	0.765	2.037±0.090	0.180±0.064	9.371±3.313	1.696	3.014
L/PW	4	1.03-1.16	–	1.088±0.032	0.064±0.022	6.208±2.195	0.159	−4.360
M_1								
L	5	1.75-2.20	–	1.920±0.077	0.172±0.054	9.393±2.970	1.347	2.099
PW	5	1.25-1.70	0.907	1.440±0.080	0.178±0.056	12.993±4.109	0.603	−0.225
AW	5	1.25-1.60	0.991	1.380±0.060	0.135±0.043	10.279±3.250	1.339	2.021
L/PW	5	1.28-1.48	–	1.339±0.037	0.083±0.026	6.495±2.054	1.747	3.022
M_2								
L	5	1.50-1.85	–	1.720±0.072	0.160±0.051	9.796±3.098	−0.753	−2.039
PW	5	1.25-1.65	0.786	1.438±0.071	0.158±0.050	11.538±3.649	0.339	−1.105
AW	5	1.25-1.60	0.672	1.400±0.057	0.127±0.040	9.561±3.023	0.905	2.000
L/PW	5	1.12-1.33	–	1.200±0.037	0.083±0.026	7.224±2.284	1.271	1.884
M_3								
L	2	1.60-1.95	–	–	–	–	–	–
PW	2	1.10-1.25	–	–	–	–	–	–
AW	2	1.10-1.25	–	–	–	–	–	–
L/PW	2	1.45-1.56	–	–	–	–	–	–

greater wear of the premolars than of the molars. Given the high probability that the deciduous posterior premolars erupted prior to the molars, the conclusion appears to be inescapable that the premolars of AMNH 12598 are deciduous. Once the morphology of this specimen is understood in an ontogenetic perspective, one is more likely to accept the conspecific nature of the Huerfano sample with that from Bridger sediments. The differences between *Uintanius ameghini* and "*Huerfanius rutherfurdi*," I believe, can be narrowed down to the differences between deciduous and permanent premolars of different geographical samples.

Uintanius vespertinus (Matthew, 1915), new combination
Figures 117, 118

?*Omomys vespertinus* Matthew, 1915, p. 450.
?*Loveina vespertina*: Simpson, 1940, p. 188.
Omomys vespertinus: Gazin, 1962, p. 32.

Type. AMNH 16835, left mandible fragment with M_{1-3}; collected from upper Gray Bull beds, Willwood Formation, at head of Elk Creek, Bighorn Basin, Wyoming.

Hypodigm. The type and AMNH 16213, from the top of the Almagre beds, San José Formation, New Mexico.

Geographical and Temporal Distribution. Wasatchian (early Eocene) of Wyoming and New Mexico.

Specific Diagnosis. Differs from *U. ameghini* in the less enlarged state of the third and fourth premolars.

Dental Formula. Probably the same as for *U. ameghini*.

Discussion. When first described by Matthew in 1915 (pp. 450-451), this species was only very tentatively referred to *Omomys*. In a footnote Simpson (1940, p. 188) allocated the species, again tentatively, to *Loveina*. Gazin (1962, p. 32) returned this taxon to *Omomys* without expressing doubt about this as Matthew did.

There is no proof that the maxilla (AMNH 16213) from the Almagre beds, bearing P^3-M^3,

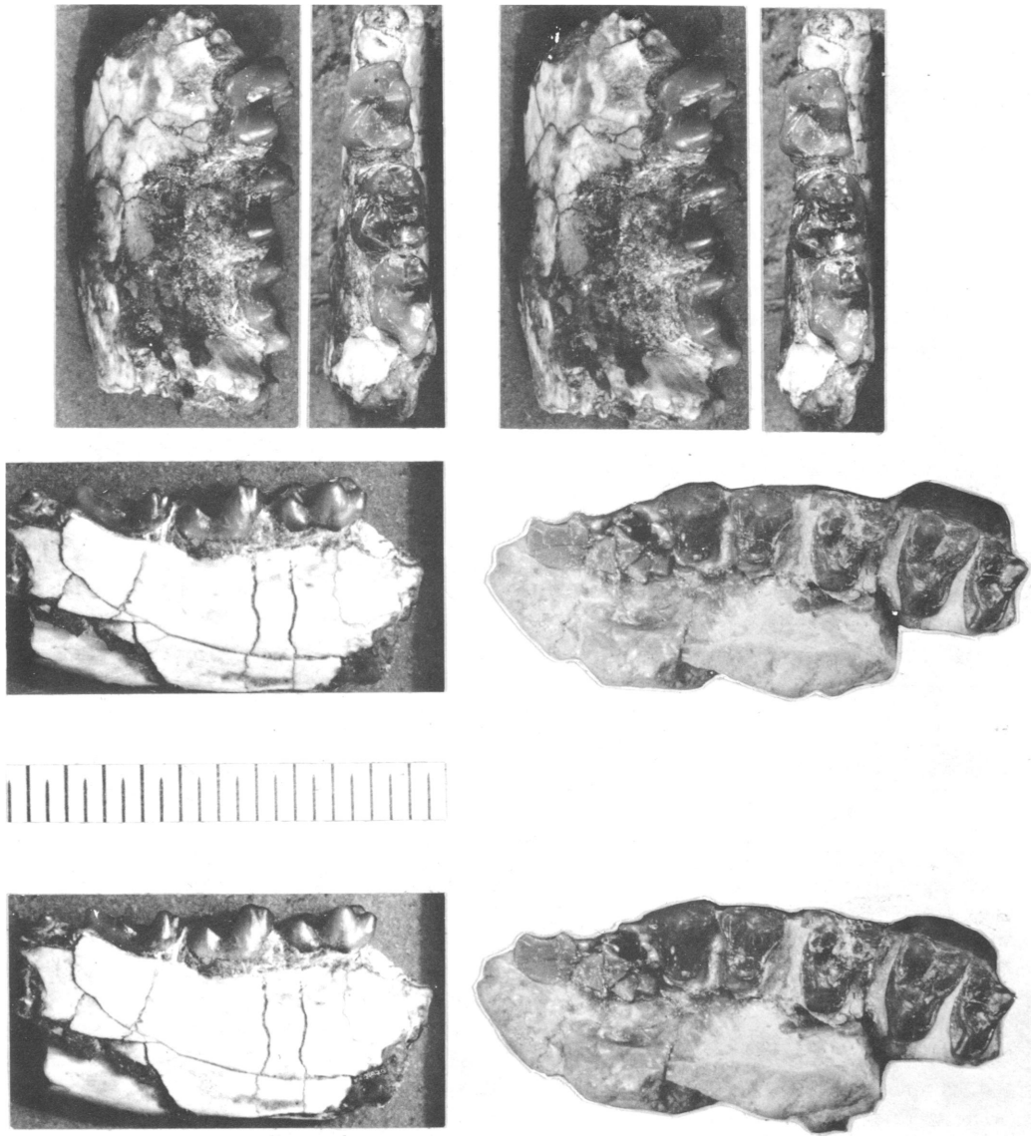


FIG. 117. *Uintanius vespertinus*, AMNH 16835, type, upper Gray Bull beds, left M_{1-3} (above and below left); and AMNH 16213, San José beds, left P^3-M^3 (below right). Stereophotographs: above left lateral, above and below right occlusal, and below left medial views. Subdivisions on scale represent 0.5 mm.

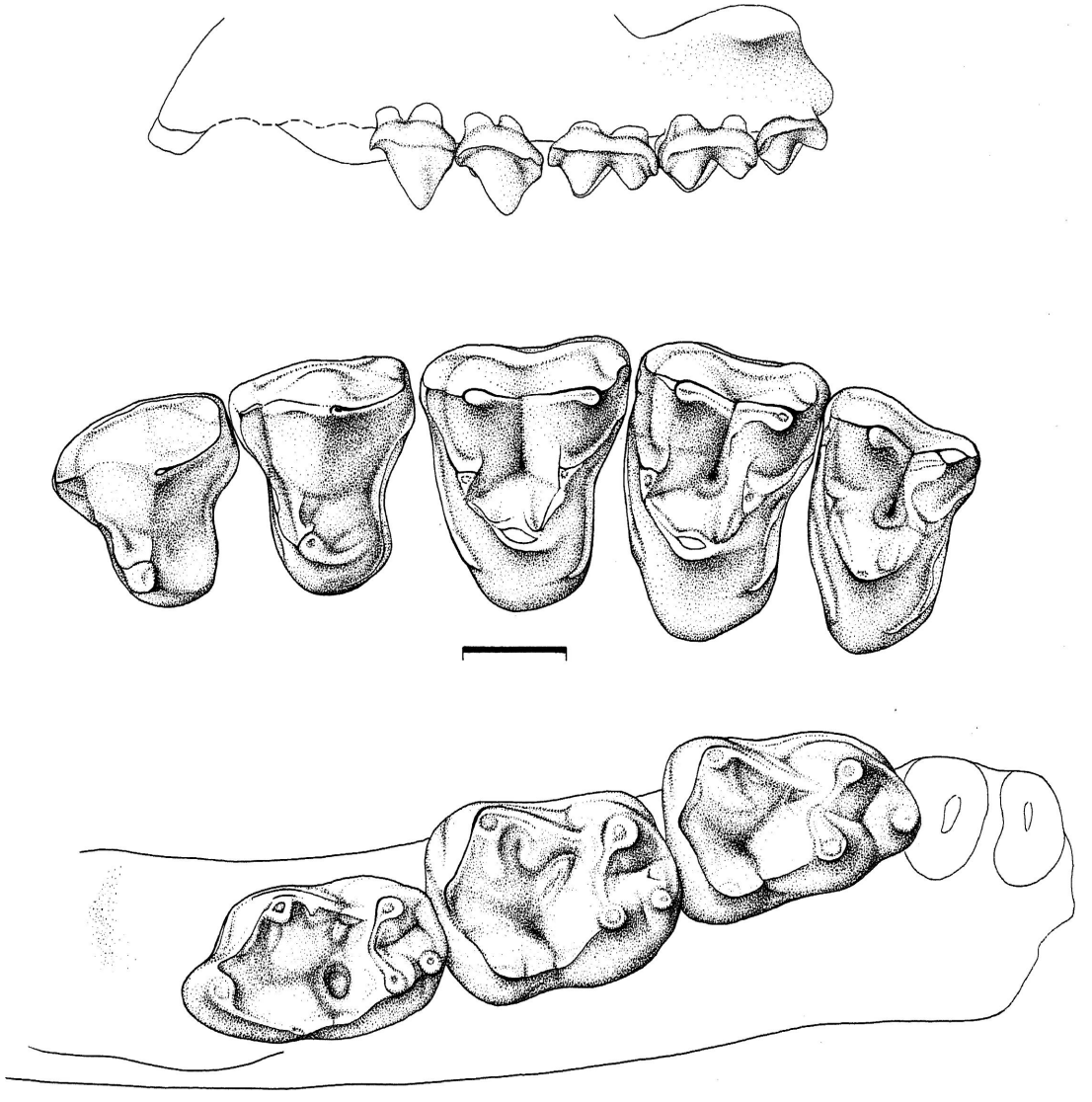


FIG. 118. *Uintanius vespertinus*, right P^3-M^3 and left M_{1-3}, based on AMNH 16213 and AMNH 16835, respectively, both Wasatchian; buccal (above) and occlusal (middle and below) views. Reconstruction shown by uniform stippling and by broken lines. Scale represents 1 mm.

originally allocated by Matthew, is of the same species as the type. I believe, however, that Matthew's original action of association in one species was probably correct because both the lower teeth (the type) and the uppers bear the same striking generic similarity to the younger *Uintanius ameghini*. Only associated upper and lower dentitions from the same beds of the two geographical areas will settle this problem.

TRIBE UTAHIINI, NEW

Type Genus. Utahia Gazin, 1958.

Included Genera. Type genus and *Stockia* Gazin, 1958.

Tribal Diagnosis. Omomyines with a derived, constricted trigonid construction and concomitant enlargement of the talonid.

Discussion. This is one of the most poorly known tribes of the family. The characteristic trigonid construction is highly diagnostic and very similar to the constricted trigonids of most platyrrhines with well-developed hypocones. This character state is perhaps tied to an adaptation in which the talonid function is much more important than that associated with the mechanics of the trigonid.

UTAHIA GAZIN, 1958

Utahia Gazin, 1958, p. 66.
Omomys: Gazin, 1962, p. 31.

Type Species. Utahia kayi Gazin, 1958.

Included Species. Type species only.

Geographical and Temporal Distribution. Late Wasatchian-earliest Bridgerian (late early Eocene-early medial Eocene) of Utah and Wyoming.

Generic Diagnosis. Omomyines with relatively large M_3 and mesiodistally constricted trigonids on M_2 and M_3.

Utahia differs from *Stockia* in having a relatively smaller P_4, higher trigonids, much less crenulated enamel, and a talonid notch which is V- to U-shaped and basally rounded; differs from both *Shoshonius* and *Washakius* in lacking a mesostylid on the lower molars.

Discussion. When Gazin (1958, pp. 66-68) described *Utahia* he suggested it to be "in many ways intermediate between *Hemiacodon* and *Washakius*." Similarities to *Loveina* were also noted. In his Chart 1 *Utahia* was derived from a *Hemiacodon* or a near-*Hemiacodon* ancestry. I do not find shared advanced similarities with *Hemiacodon*. Both *Utahia* and *Washakius* have distinct, derived features of their own. *Utahia*, as *Stockia*, has strongly constricted trigonids on M_2 and M_3, a character unlike the more ancestral omomyine condition shown by *Washakius*. The latter has the derived lower molar metastylids not present in *Utahia*. I am convinced that *Utahia* is most closely related to *Stockia*.

Comparisons of *Utahia* and *Stockia* are hindered by the fact that the only good specimen of the former is the generoholotype with considerably worn teeth, whereas the *Stockia* material consists largely of unworn teeth. The specific distinction of the two samples is not in question because in spite of the differences in wear, the diagnostic features are relatively clear cut. I would, however, question the taxonomic value of slightly higher trigonids and lack of crenulations along with some apparent differences in the shape of the talonid notch of *Utahia* as sufficiently different attributes to warrant generic separation of *Stockia*. In light of the lack of information on the anterior dentition and upper teeth and the existing differences between the lower teeth of the two samples I continue the maintenance of separate generic rankings.

Adaptations. The sample is very limited and consequently any comments on adaptations are of very tentative nature. The most striking character of *Utahia*, as well as *Stockia*, lies in the very open M_1 trigonid on the one hand and the mesiodistally constricted and lingually closed M_{2-3} trigonids on the other. Correlated with this are the relatively large talonids of the last two molars. The only mandible fragment known with well-worn teeth is not unusually thick mediolaterally. Unusually heavy stressing in a transverse direction, therefore, appears to have been unlikely as a habitual mode of mastication. The reduction of the trigonids suggests reduction in the components usually involved in shear when the mandible is moved in an orthal direction.

The meager evidence perhaps suggests frugivo-

TABLE 25
Numerical Data for Specimens of *Utahia kayi*

	CM 6488 (type)	CM 6416	CM 6412	CM 13242	CM 6411	USNM 22384	USNM 19197	*N*	OR	M
P_4										
L	1.62	–	–	–	–	–	–	1	–	–
PW	1.30	–	–	–	–	–	–	1	–	–
M_1										
L	1.82	–	–	1.85	–	–	–	2	1.82-1.85	1.83
PW	1.35	–	–	1.50	–	–	–	2	1.35-1.50	1.42
AW	1.45	–	–	1.45	–	–	–	2	1.45	1.45
M_2										
L	1.85	1.85	–	–	–	2.12	–	3	1.85-2.12	1.94
PW	1.62	1.75	–	–	–	1.80	–	3	1.62-1.80	1.72
AW	1.50	1.65	–	–	–	1.71	–	3	1.50-1.71	1.62
M_3										
L	2.42	2.50	2.35	–	–	2.62	2.51	5	2.35-2.62	2.48
PW	1.50	1.50	1.50	–	–	1.50	1.53	5	1.50-1.53	1.51
AW	1.38	1.50	1.42	–	–	1.57	1.54	5	1.38-1.54	1.48
M^1										
L	–	–	–	–	1.60	–	–	1	–	–
AW	–	–	–	–	2.00	–	–	1	–	–

rous-insectivorous adaptation, although a knowledge of the anterior dentition may considerably alter this hypothesis.

Utahia kayi Gazin, 1958
Figures 119-121; Table 25

Utahia kayi Gazin, 1958, p. 67.
Omomys sheai Gazin, 1962, p. 31.

Type. CM 6488, right mandible fragment with P_3-M_3; collected from the Powder Wash locality of the Carnegie Museum, T.7, 5, R. 25 E, Utah.

Hypodigm. The type and CM 6412, 6416, 13242, 19197, from the type locality; USNM 22384 from Wasatch beds (Lost Cabin equivalents) in the vicinity of La Barge and Big Piney, Sublette County, Wyoming.

Geographical and Temporal Distribution. Same as for genus.

Specific Diagnosis. Only known species of the genus.

Dental Formula. Cannot be determined from the known material.

Discussion. CM 6411 is an upper molar (probably M^1), identified by Gazin (1958) as belonging to *Utahia kayi*. It can be allocated to *Uintanius*, cf. *U. ameghini*.

STOCKIA GAZIN, 1958

Stockia Gazin, 1958, p. 68.

Type Species. *Stockia powayensis* Gazin, 1958.

Included Species. Type species only.

Geographical and Temporal Distribution. Early Uintan (early late Eocene) of California.

Generic Diagnosis. Omomyines with very crenulated enamel, mesiodistally constricted trigonids on the last two molars, and a relatively long last molar. Clearly separable from *Hemiacodon* in having a relatively taller P_4, relatively less wide talonid, and a paraconid on both M_2 and M_3 that is close and directly mesial to the trigonid notch. *Stockia* differs from *Utahia* in having a relatively taller P_4, more crenulated enamel, a more lingually placed paraconid on P_4,

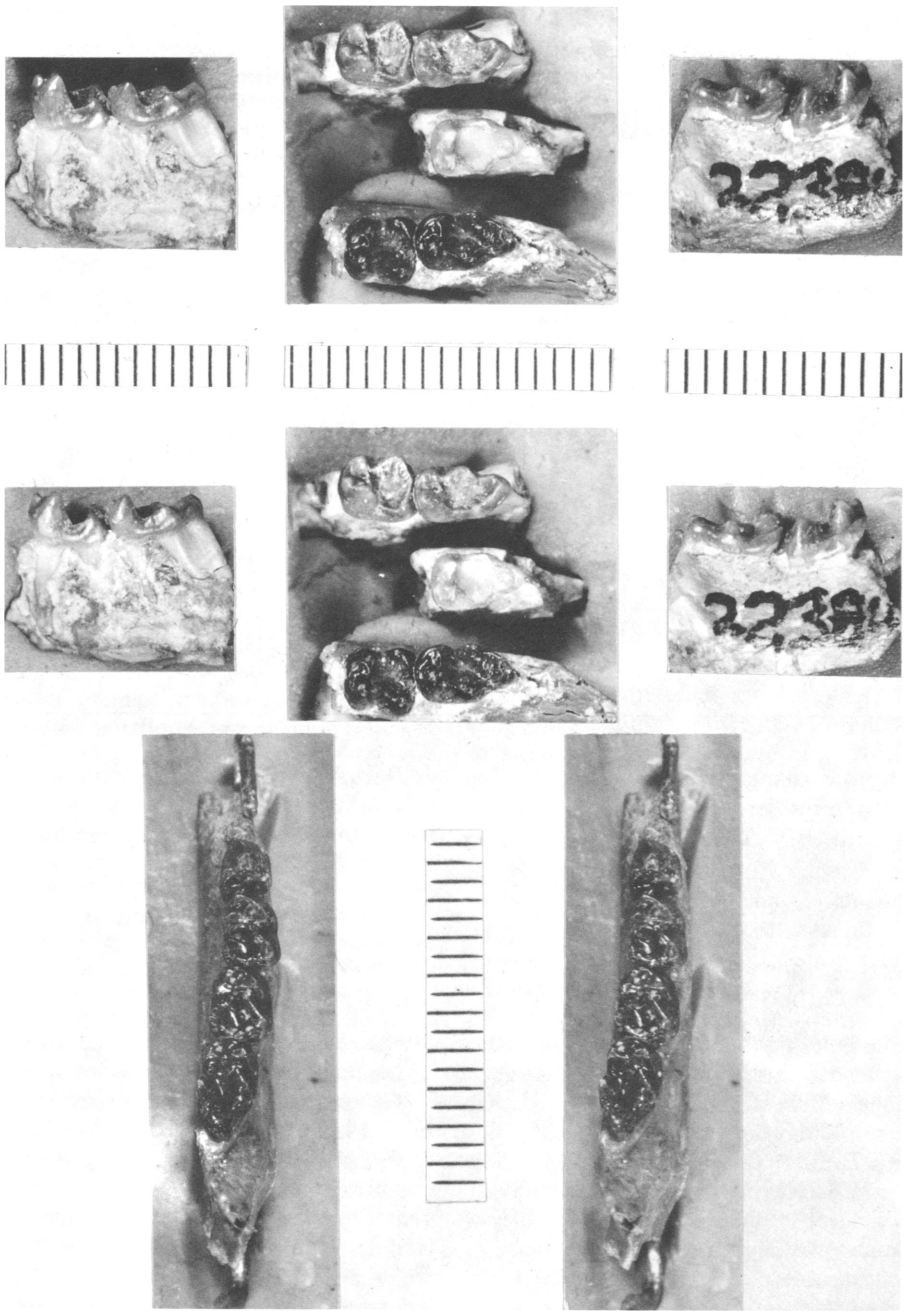


FIG. 119. *Utahia kayi*, USNM 22384, type of "*Omomys sheai*," upper Wasatch beds, upper Green River Basin, right M_{2-3} (above left, above top, and above right); CM 19197, Powder Wash, Green River beds, left M_3 (above middle center); CM 6416, Powder Wash, left M_{2-3} (above middle bottom); and CM 6488, type, Powder Wash, Green River beds, left P_3-M_3 (below). Stereophotographs: above middle and below occlusal, above left medial, and above right lateral views, respectively. Subdivisions on scales represent 0.5 mm.

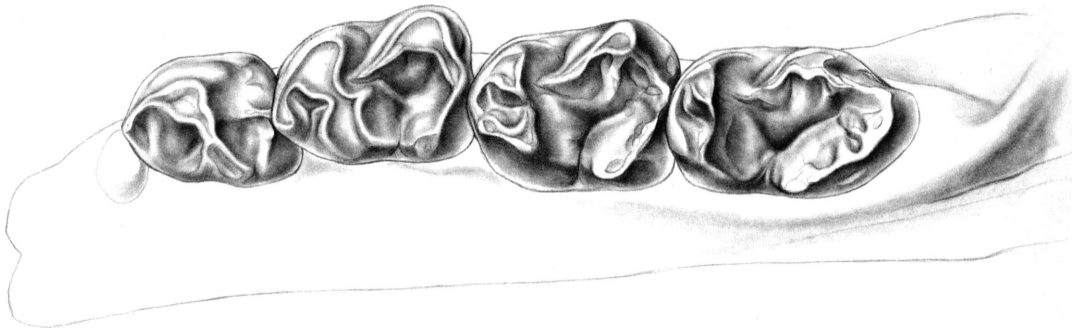


FIG. 120. *Utahia kayi*, CM 6488, type, early Bridgerian, Wyoming, right mandible fragment with P_4-M_3; occlusal view. Scale represents 1 mm.

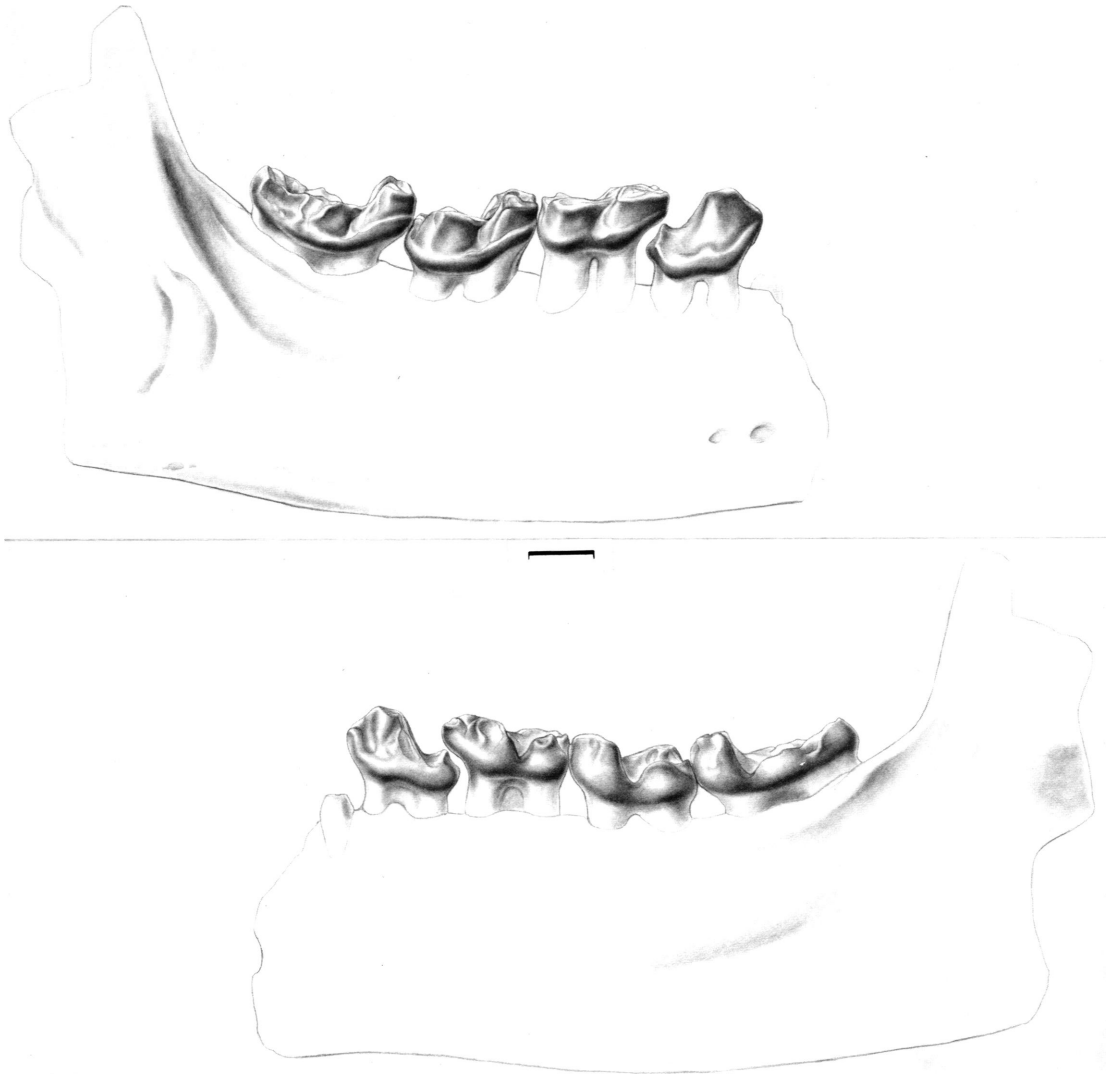


FIG. 121. *Utahia kayi*, CM 6488, type, early Bridgerian, Wyoming, right mandible fragment with P_4-M_3; lateral (above) and medial (below) views, respectively. Scale represents 1 mm.

and a talonid notch which is very narrow and very constricted basally.

Discussion. *Stockia* was characterized by Gazin (1958, pp. 68-70) as a genus very near *Hemiacodon*, and probably derived from *Utahia*. Chart 1 of that paper and figure 14 of Russell, Louis, and Savage (1967) show *Stockia* derived directly from *Utahia*. As far as I can judge, this is a taxon distinct on the generic level from other known omomyines, including *Utahia*, although it probably shared a more recent common ancestor with the latter than with any other genus known.

Adaptations. P_4 is tall, distinctly higher than any of the molars. There is a small, lingually turned paracristid-paraconid on that premolar and a broad distal shelf. The most characteristic

TABLE 26
Numerical Data for Specimens of *Stockia powayensis* from Sandstones Associated with the Poway Conglomerate

	LACM 2234	LACM 17322	LACM 2235	*N*	OR	M
P_4						
L	–	2.28	–	1	–	–
PW	–	1.62	–	1	–	–
M_1						
L	–	2.92	–	1	–	–
PW	2.20	2.40	–	2	2.20-2.40	2.30
AW	–	2.05	–	1	–	–
M_2						
L	2.78	–	2.78	2	2.78	2.78
PW	–	–	2.53	1	–	–
AW	2.10	–	2.40	2	2.10-2.40	2.25
M_3						
L	2.96	–	3.15	2	2.96-3.15	3.50
PW	1.92	–	–	1	–	–
AW	1.68	–	2.10	2	1.68-2.10	1.89
M^3						
L	2.80	–	–	1	–	–
PW	1.77	–	–	1	–	–
AW	1.50	–	–	1	–	–

features of the molars are their crenulated enamel and the bucally open trigonid of M_1 in contrast with the mesiodistal constriction of the last two teeth in *Utahia*. This trigonid reduction is extreme, particularly in contrast with the long and wide talonids. The talonid notches of the molars are narrow at both the distal base of the metaconid and the mesial portion of the entocristid. The known mandible fragments are very thin mediolaterally and relatively deep, indicating, as in *Utahia*, a relative absence of unusually forceful mediolateral stressing by the pterygoid-masseter-temporal muscle complex.

The crenulations on the molars perhaps indicate an adaptation to increase the surface area of the talonids. It is in this respect that the crenulations represent additional sharp edges which facilitated division of the food.

The tall P_4 and the somewhat unusual low-crowned molars might have evolved as a response for a frugivorous, perhaps even nectarivorous, type of diet. None of these characters in the conbination that they appear in *Stockia* suggest adaptations either for insectivory or folivory.

Stockia powayensis Gazin, 1958
Figures 122, 123; Table 26

Stockia powayensis Gazin, 1958, p. 70.

Type. LACM 2235, right mandible with M_{1-3}; collected from white sandstones associated with the Poway conglomerate exposed on the west bank of San Diego River, approximately ¼ mile north and east of San Diego Mission, CIT Vert. Paleo. loc. 249, San Diego County, California.

Hypodigm. The type and LACM 17322 from the type locality and LACM 2234.

Geographical and Temporal Distribution. Same as for genus.

Specific Diagnosis. Only known species of the genus.

Dental Formula. Cannot be determined from the known material.

Discussion. *Stockia powayensis* is poorly known, and in addition to two jaw fragments with three (LACM 2234) and two (LACM 2235) teeth, respectively, there are only three additional teeth known to me. Two of these (LACM 17322) appear to be M_1, although one of them

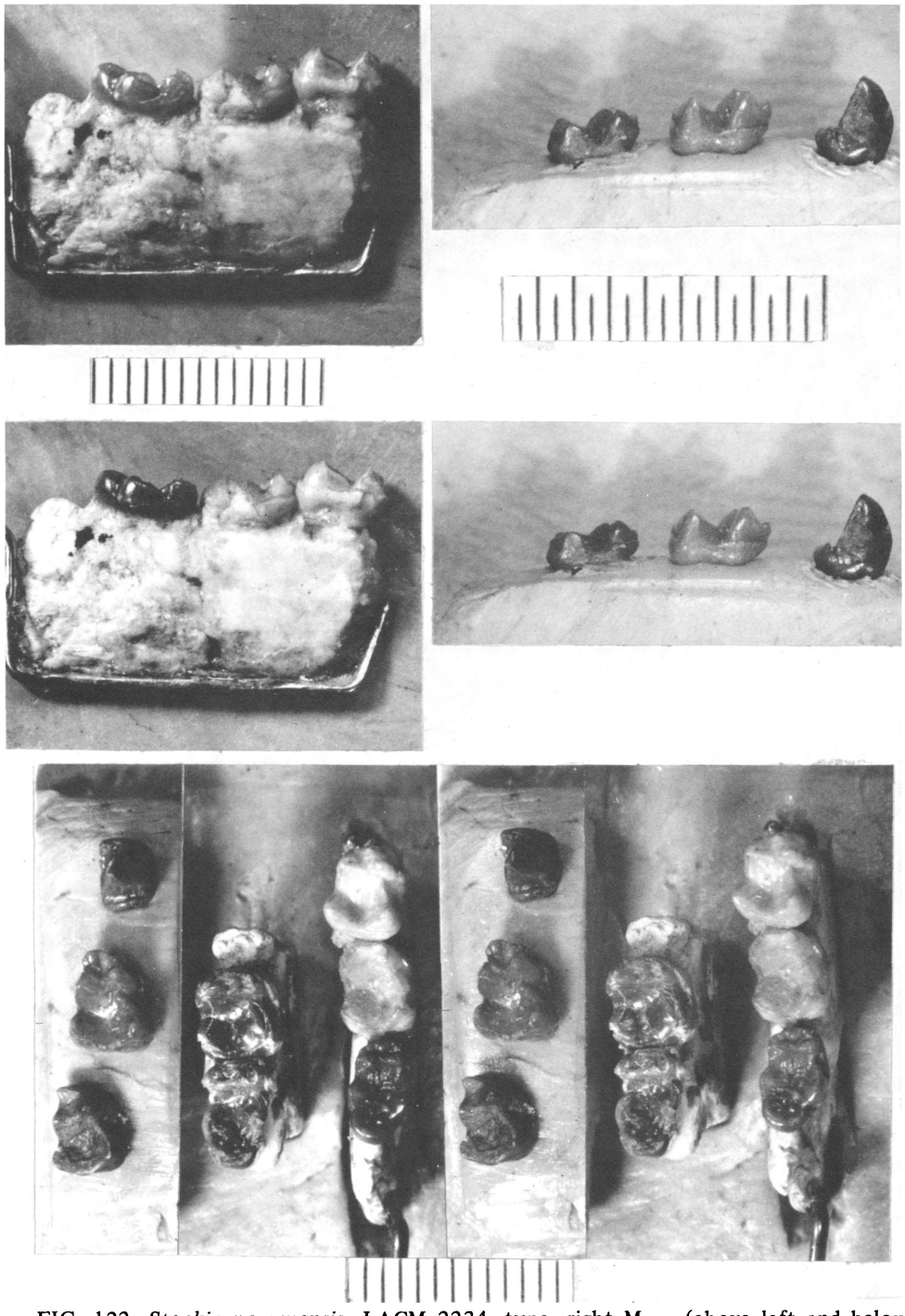


FIG. 122. *Stockia powayensis*, LACM 2234, type, right M_{1-3} (above left and below right); LACM 2235, right M_{2-3} (below center); and LACM 17322, right P_4, either right dP_4 or M_1, and right M_1 (above right and below left); all from Poway beds. Stereophotographs: above lateral and below occlusal views. Subdivisions on scales represent 0.5 mm.

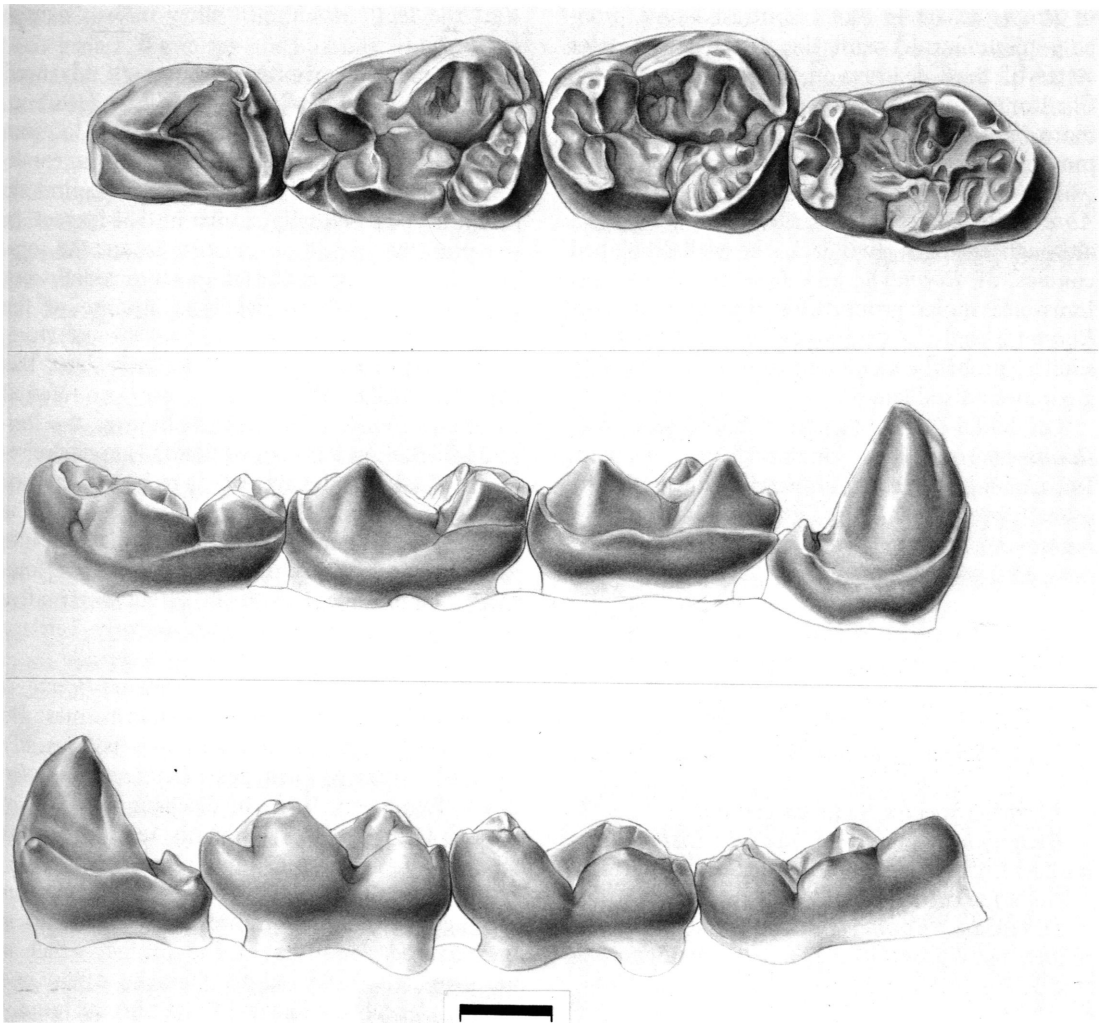


FIG. 123. *Stockia powayensis*, right P_4-M_3, based on LACM 17322 (P_4) and LACM 2234 (M_{1-3}), Uintan, California; occlusal (above), buccal (middle), and lingual (below) views. Scale represents 1 mm.

could possibly be a dP_4, although I doubt this. One P_4 (LACM 17322) is known, which probably can be allocated to this taxon.

TRIBE ROONEYIINI, NEW

Type Genus. Rooneyia Wilson, 1966.

Included Genera. Type genus only.

Tribe Diagnosis. Omomyids with compact, low-crowned, robust molars. These have cuspate, exceptionally developed conules and a hypocone on the postcingulum almost equal in size to the protocone. In addition to these characters distinguishing them from all other omomyids, rooneyiinines have two premolars and a small canine. Unlike that on known skulls of anaptomorphines and microchoerines, the petromastoid is not inflated.

Discussion. Dental comparisons of *Rooneyia* with the genera *Callicebus* and *Aotes* have proved very interesting although at the outset it must be clearly stated that the presence of two premolars in the first and three in the last two genera precludes any ancestor-descendant relationships. Furthermore, the elongated ectotympanic, lack of orbital funnels, and the less encephalized brain

of *Rooneyia* are in direct contrast (some probably plesiomorph) with the different character states of these features in platyrrhines. Yet the Chadronian primate, with the exception of its more reduced antemolar dentition, is in general more primitive than the platyrrhine morphotype.

I find the development of the hypocone in *Aotes* and *Callicebus* similar to that in *Rooneyia*, although the first two lack the well-developed conules of *Rooneyia* and have advanced, less transverse molar proportions. The premolars of *Rooneyia* and the extant genera noted are quite similar, probably stemming from their relatively great mesiodistal length.

On dental characters alone tribal separation of *Rooneyia* from other omomyids is warranted. Recognizing the rooneyiinines, in addition to the other tribes of the Omomyinae, allows the taxonomic expression of diversity of the Omomyinae compared with the Anaptomorphinae.

ROONEYIA WILSON, 1966

Rooneyia Wilson, 1966, p. 228.

Type Species. Rooneyia viejaensis Wilson, 1966.

Included Species. Type species only.

Geographical and Temporal Distribution. Earliest Chadronian (earliest Oligocene) of Texas.

Generic Diagnosis. Only known genus of tribe.

Discussion. Rooneyia has been expertly described by Wilson (1966), and the endocast was studied by Hofer and Wilson (1967), and Radinsky (1970).

I agree with the details of the description of the teeth by Wilson, yet I disagree with his systematic assessment. He considered the molars of *Rooneyia* to be primitive in pattern (presumably among the omomyids) and stated that (p. 232), "Had they been found alone, they might have been referred to any one of several genera." The low-crowned bulbous cusped molars, M^{1-2}, with their large hypocones are distinct and unique among the Omomyidae. Had we a better record of the crania in the Omomyidae, I suspect that many of the cranial characters, such as the contact patterns of the orbital bones and the configuration of the basicranial morphology, might turn out to be quite primitive for the family. Yet, the teeth would still allow us to diagnose *Rooneyia*.

In discussing primitive primate vs. advanced primate features of *Rooneyia*, Wilson (1966, p. 242) listed the position of the foramen lacerum posterior as advanced over the lemuriform condition. I find both the strepsirhine and haplorhine morphotype essentially similar in that respect. In the primitive condition of both groups the foramen lacerum posterior is posteromedial, not posterolateral. Wilson listed an absence of the foramen lacerum medium as an advanced feature. All lemuriforms and all haplorhines lack this opening outside the bulla. What has been referred to as the foramen lacerum medium in the lorisoids (including the cheirogaleids) is argued elsewhere (Szalay and Katz, 1973) to be the anterior carotid foramen, not a strict homologue of the promontory foramen or of the foramen lacerum medium. Thus, the absence of the human foramen lacerum medium is in effect a primitive character among the primates or early Tertiary Eutheria.

Wilson (1966) originally considered *Rooneyia* to be within the infraorder Lemuriformes. He tentatively suggested that *Rooneyia* is "possibly derivable from a form near *Hemiacodon*." (p. 244). Two years later, in discussing *Rooneyia*, Simons (1968, p. 11) summarily referred to it as an early Oligocene catarrhine from Texas.

The most compelling dental argument concerning the omomyid affinities of the genus is the reduced condition of the canine, which is unfortunately not a unique character of any one of the dental complexes found in the group.

The size of the canine and the nonlemuriform character of the basicranium represent a combination that indicates an omomyid stamp more than any other family level ties. Unlike the extreme inflation of the mastoid in *Tetonius*, an anaptomorphine, and *Necrolemur*, a microchoerine, the moderate mastoid inflation of *Rooneyia* suggests omomyine derivation. The relatively large M^3 and a hypocone development reminiscent of *Washakius* appear to confirm the subfamily ties of *Rooneyia*.

The assessment by Simons (1968, p. 11) that *Rooneyia* is a Texan catarrhine may perhaps be explained by the convergent similarity of the upper molars to those of *Apidium* (for illustra-

tion of the latter, see Simons, 1972, fig. 76). In both genera the cusps are bulbous, the conules large, and the hypocone enlarged. The mesial and distal cusps (paracone, paraconule, protocone vs. metacone, metaconule, hypocone) are aligned in two rows more or less parallel to each other. This structurally pre-cercopithecid arrangement of the molar relief is similar in *Rooneyia* to that of the catarrhine *Apidium* and probably to the more derived *Parapithecus*. Unlike the premolars of the Fayum *Apidium*, those of *Rooneyia* do not have the enlarged paraconules and, of course, the Texan primate has one less premolar and a relatively smaller canine.

Adaptations. The extent of the dental arch and the approximate size and estimated area of the individual molars in *Rooneyia viejaensis* are about the same as those of *Aotes trivirgatus*. The relative size of the orbits and the brain, however, are strikingly smaller in *Rooneyia*. Judged from the position of the foramen magnum the skull of the Texas primate is only very slightly kyphosed, much less than in callithricids (*Callithrix jachus*, for example) with a comparable endocranial volume.

A large flange of the frontal descends behind the orbits. Judged from the postorbital constriction of the skull, part of the major mass of the temporalis muscle extended slightly anteriorly above the orbits. In the case of *Rooneyia* the orbital partition, perhaps the homologue of that part of the postorbital funnel in *Tarsius*, platyrrhines, and catarrhines, appears to be the bony wall which kept the muscle from intruding into the orbit. Possibly this partition is the initial adaptation responsible for the role of protecting the eyeballs and associated structures from the contraction of the temporalis.

The relative size of the orbits of *Rooneyia* is difficult to assess. If one were to plot the length of the skull against the diameter of the orbits, as Walker did (1967) for the Malagasy lemurs, and plot it on this author's graph, *Rooneyia* would fall, as suggested by Simons (1972), with the nocturnal forms. Yet the orbits of *Rooneyia* are not relatively very large and it is not unlikely that its orbit-to-skull length proportions are primitive features from a relatively much larger-eyed ancestry.

Unlike in other known omomyids, the tooth rows appear to be more widely separated in *Rooneyia*. The known teeth show a combination of characters not known to me in any primarily insectivorous or carnivorous primate. The cusps are rounded, not very pointed, and the crests are very broadly based, not high. The cusps and cuspules are greatly expanded, swollen so they touch each other at their base.

I judge that *Rooneyia* was primarily frugivorous.

Rooneyia viejaensis Wilson, 1966
Figures 124-128, 143, 146

Rooneyia viejaensis Wilson, 1966, p. 228.

Type. UTBEG 40688-7, almost complete, uncrushed skull, lacking premaxillaries, the posterior portions of the parietals, and the zygomatic arches; collected from Chambers Tuff Formation, Vieja Group, Rifle Range Hollow, Presidio County, Texas.

Hypodigm. Type only.

Geographical and Temporal Distribution. Same as for genus.

Specific Diagnosis. Only known species of the genus.

Dental Formula. $I\frac{1,2}{1,2}; C\frac{1}{1}; P\frac{3,4}{3,4}; M\frac{1,2,3}{1,2,3}$.

Discussion. Wilson (1966) gave a detailed account of the locality of the holotype of *Rooneyia*, its stratigraphic position, and its age. He stated that (p. 229), "The Chambers Tuff must be very close to 35 m.y." As noted above, the description of the teeth and cranium are excellent and therefore the specimen needs no redescription.

Measurements of the skull and teeth can be found in Wilson (1966).

SUBFAMILY **EKGMOWECHASHALINAE**, NEW

Type Genus. Ekgmowechashala Macdonald, 1963.

Included Taxa. Type genus only.

Geographical and Temporal Distribution. Early Arikareean (late Oligocene) of South Dakota and Oregon.

Subfamily Diagnosis. The Ekgmowechashalinae, represented by one species, differs from other omomyids in having an $M_1 > M_2 > M_3$ size relationship, peculiarly flattened molars, a large,

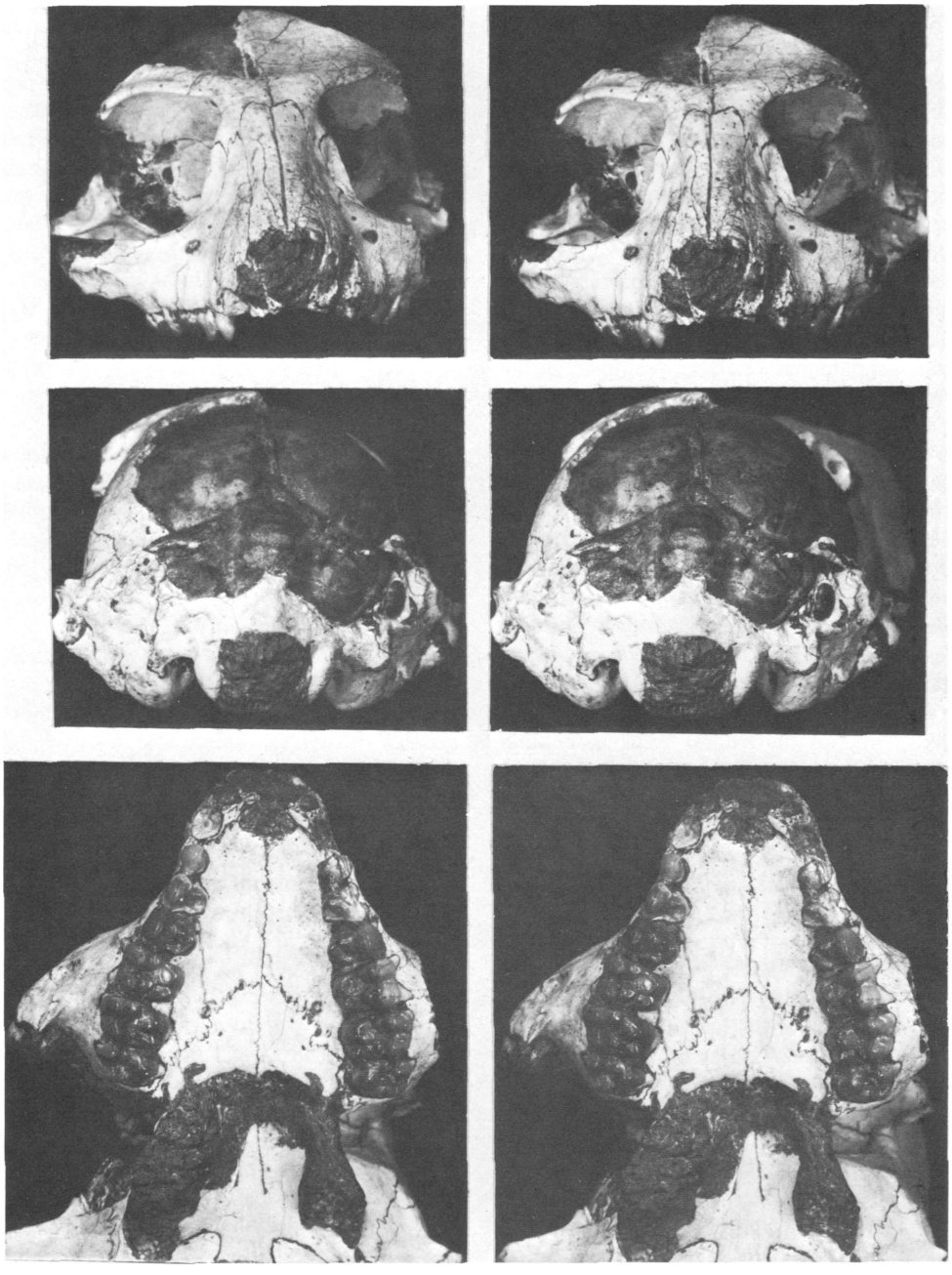


FIG. 124. *Rooneyia viejaensis*, UTBEG 40688-7, type, Chambers Tuff beds, cranium. Stereophotographs: above frontal and middle posterior views of the skull, and below ventral view of palate and dentition.

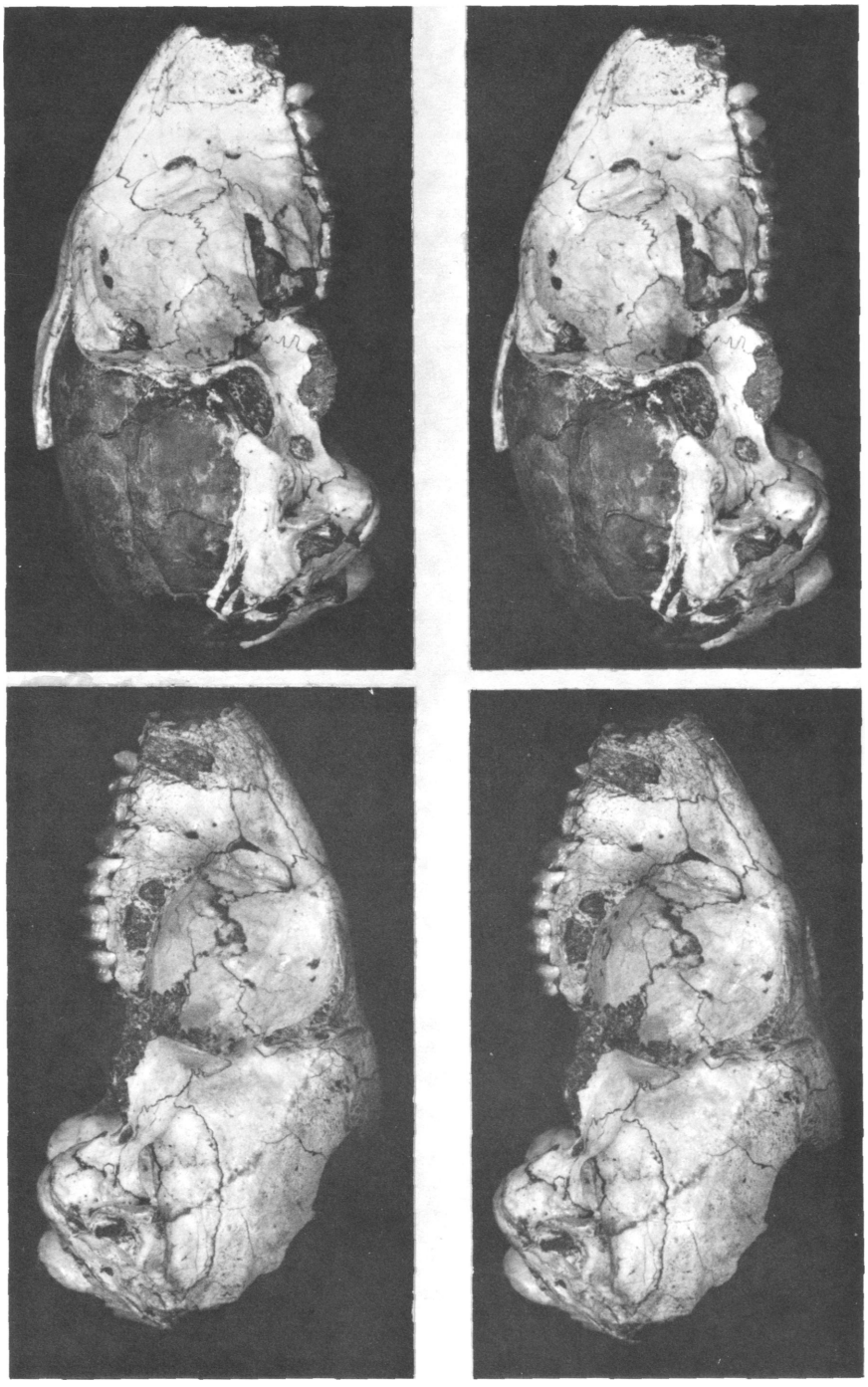


FIG. 125. *Rooneyia viejaensis*, UTBEG 40688, type, Chambers Tuff beds, cranium. Stereophotographs: above right lateral, below left lateral views, respectively.

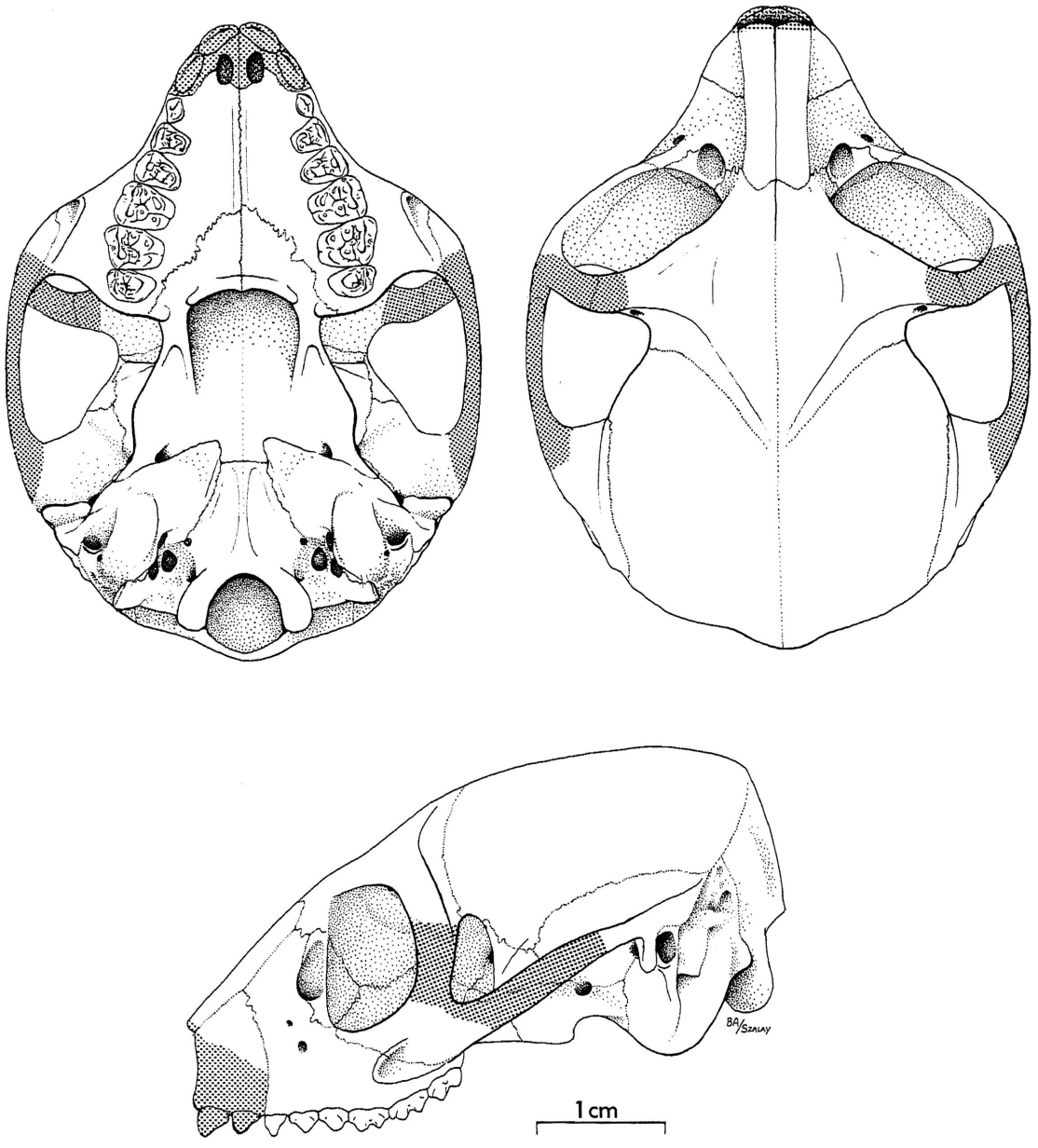


FIG. 126. *Rooneyia viejaensis*, cranium based on UTBEG 40688-7, type, early Chadronian of Texas; ventral (above left), dorsal (above right), and lateral (below) views. Reconstruction shown by uniform stippling.

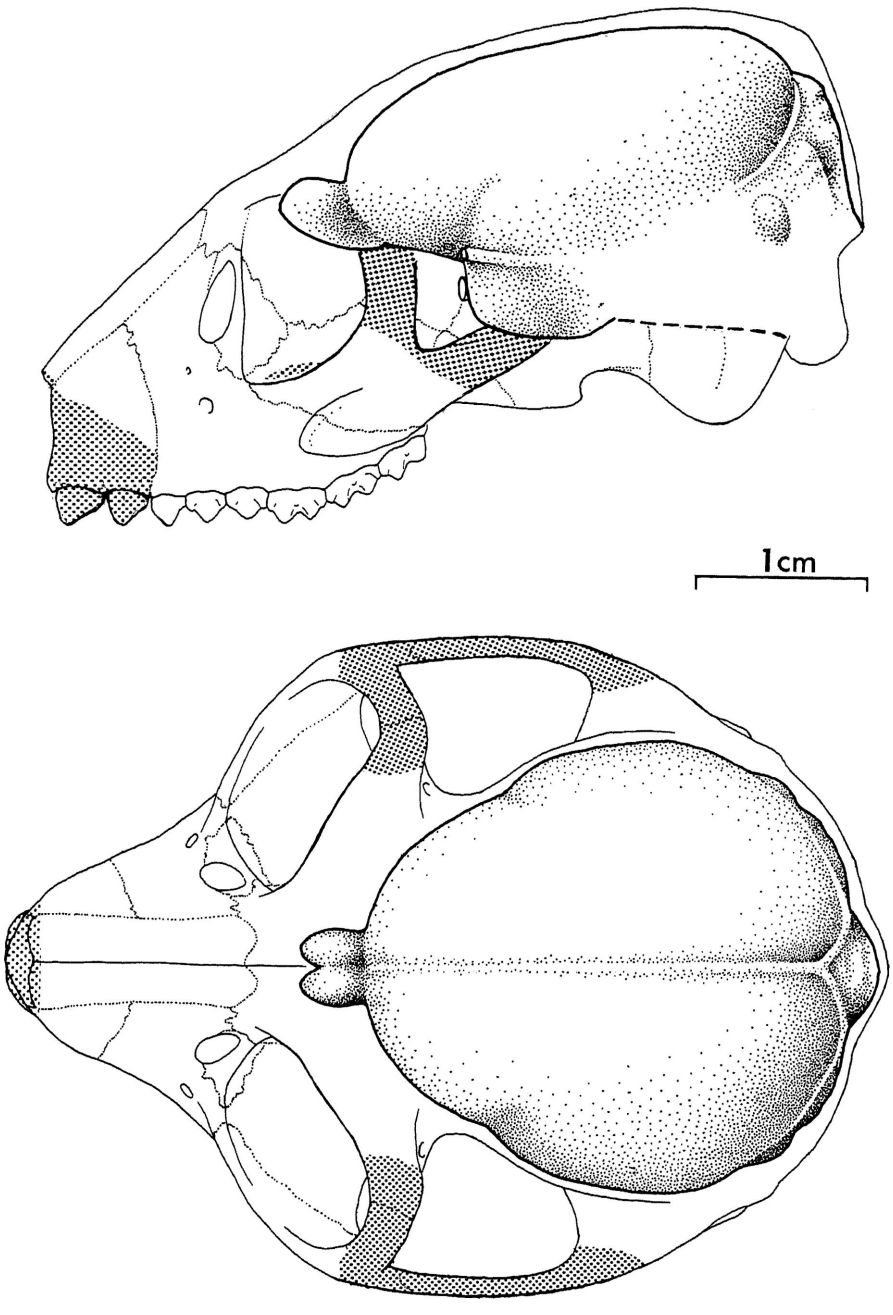


FIG. 127. *Rooneyia viejaensis*, lateral and dorsal views to show endocast within cranium, based on UTBEG 40688-7, type, early Chadronian of Texas. Reconstruction is shown by uniform stippling and broken lines.

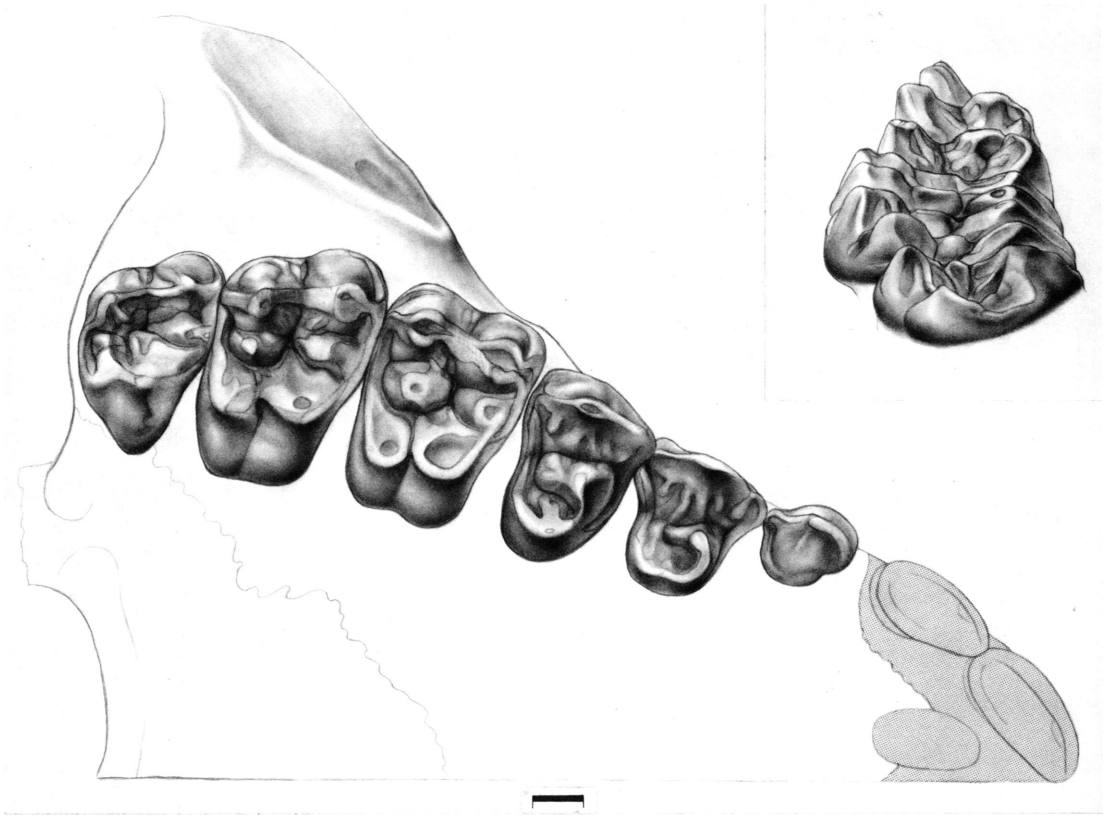


FIG. 128. *Rooneyia viejaensis*, right C-M^3, based on UTBEG 40688-7, type, early Chadronian of Texas; occlusal (left) and distal (right) views. Scale represents 1 mm.

molarized fourth premolar, and large, closely twinned entoconid and metastylid. Unlike in other omomyids, except in some microchoerines, the molar paraconids are completely reduced and the paracristid is indistinguishable from the precingulid. The degree of reduction of the two incisors, coupled with a relatively much larger canine is unique within the Omomyidae. The mandibular symphysis of the type genus, in lacking any traces of distinguishable inferior or superior transverse tori, is significantly different from the symphysis of any other known omomyid.

Discussion. The Ekgmowechashalinae is distinct from members of the Anaptomorphinae, Omomyinae, and Microchoerinae and the differences displayed by the type genus warrant the recognition of a new subfamily. The morphology of *Ekgmowechashala* is discussed under the genus and it is pertinent to the subfamily diagnosis and discussion.

EKGMOWECHASHALA MACDONALD, 1963

Ekgmowechashala Macdonald, 1963, p. 171.

Type Species. Ekgmowechashala philotau Macdonald, 1963.

Included Species. Type species only.

Geological and Temporal Distribution. Same as for the subfamily.

Generic Diagnosis. Same as for the subfamily.

Discussion. As its name would suggest, *Ekgmowechashala* is surely one of the most unusual fossil primates. It has been described in detail by its discoverer Macdonald (1963, pp. 171-173; 1970, pp. 24-25) and allocated to the

Omomyidae. Macdonald compared *Ekgmowechashala* with microchoerines, *Washakius*, *Dyseolemur*, *Stockia*, *Ourayia*, and *Chumashius*. He noted that none of the listed genera could be ancestral to it, as each depicted trends similar to parts of the character complex of *Ekgmowechashala*.

Judged from the inferred occlusal relationships of the lower teeth, the ancestry of *Ekgmowechashala* was very likely near the genus *Rooneyia*.

Adaptations. The known morphology of the dentition is unique among the primates. The first molar is the largest tooth and those following it diminish in size. The talonid portion of P_4 is enlarged, whereas the trigonid area holds a subequal protoconid and metaconid. The size difference of P_3 is relatively abrupt compared with P_4; it is distinctly smaller and premolariform. P_2 is slightly smaller but similar to P_3, and both are double rooted. The canine, judged from its alveolus, was larger than P_2 and roundly based. The incisor alveoli show the two incisors to have been very small and the roots constricted, not unlike the roots of some of the lemurid toothcombs, although I do not suggest a functional parallel.

The cheek teeth, in general, are very low-crowned, buccally and mesially bordered by cingula, and the occlusal surfaces are heavily etched by a dendritic system of grooves. The hypoconid occupies the distobuccal corner of rather square first and second molars, and the entoconid and a robust metastylid are closely twinned on the middle of the lingual border. The result of this latter twinning is a lingual profile of two notches and three cusps for each tooth. The paraconids are completely lost, the functional unit on the trigonid of the molars being the vague ridge formed by the protoconid and the wedge-shaped metaconid.

There appears to be a small mesoconid on M_1, both on SDSM 5550 and 55111. Upper teeth of this species are known from the John Day Formation, Oregon, but they have not been described.

The coronoid process was apparently very high and there are indications on the best specimen, SDSM 62104, that the mandibular angle was quite expanded. The moderately deep mandible is unusually thin transversely, indicating a minimum of requirements to withstand transversely directed forces.

The mandibular symphysis, well displayed on LACM 9207, is the most unusual among the omomyids. It was certainly not synostosed, and it has the outline of a very flat ellipse. There is no sign of a superior transverse torus and the usual pocket on the ventral part of the symphysis for the genioglossus and geniohyoid muscles is missing. The diagnostic insertions appear to have been slightly behind the inferior border of the symphysis.

The low-crowned, but broad cheek teeth along with the mandible structure suggest a diet that was neither hard nor poor in nutrients so that it did not require large daily portions. The cuspate, crenulated, low-relief molars and the molarized fourth premolar suggest adaptations for crushing not very fibrous materials and hence probably reflect specializations for frugivory.

The dentition of *Ekgmowechashala*, at least the cheek teeth, closely parallels in a convergent manner those of *Bassaricyon*, the cuataquil (R. Tedford, personal commun.), an arboreal procyonid reported to be frugivorous.

Ekgmowechashala philotau Macdonald, 1963
Figures 129-134; Table 27

Ekgmowechashala philotau Macdonald, 1963, p. 171.

Type. SDSM 5550, left mandible fragment with P_3-M_2; collected from SDSM loc. V541, Sharps Formation, late Oligocene.

Hypodigm. The type and SDSM 5551, 62104, 6242, 6247, 9207, and AMNH (Frick) 50344, all from the Sharps Formation or equivalent beds.

Geographical and Temporal Distribution. Same as for the genus.

Specific Diagnosis. Only species of the genus.

Dental Formula. $I^{1,2}_{1,2}; C^{1}_{1}; P^{2,3,4}_{2,3,4}; M^{1,2,3}_{1,2,3}$.

Discussion. See under genus.

FAMILY AND SUBORDER UNCERTAIN

DONRUSSELLIA, NEW GENUS

Teilhardina? Russell, Louis, and Savage, 1967, p. 5.

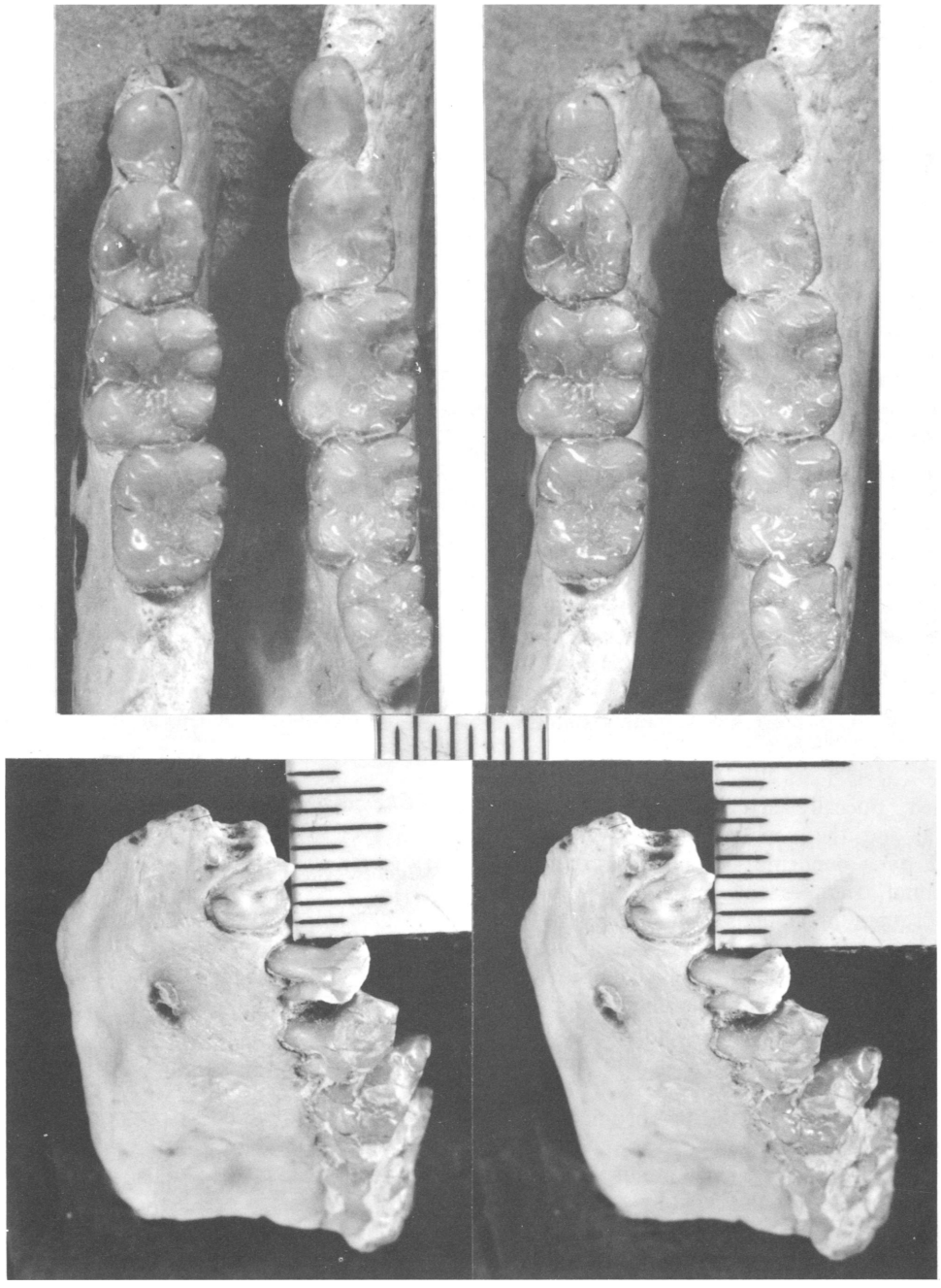


FIG. 129. *Ekgmowechashala philotau*, SDSM 5550, type, left P_3-M_2 (above left); SDSM 62104, left P_3-M_3 (above right); and LACM 9207, left alveoli for I_1 and I_2, C root, and P_2-M_2 (below); all from Sharps beds. Stereophotographs: above occlusal and below anterior views. Subdivisions on scales represent 0.5 mm.

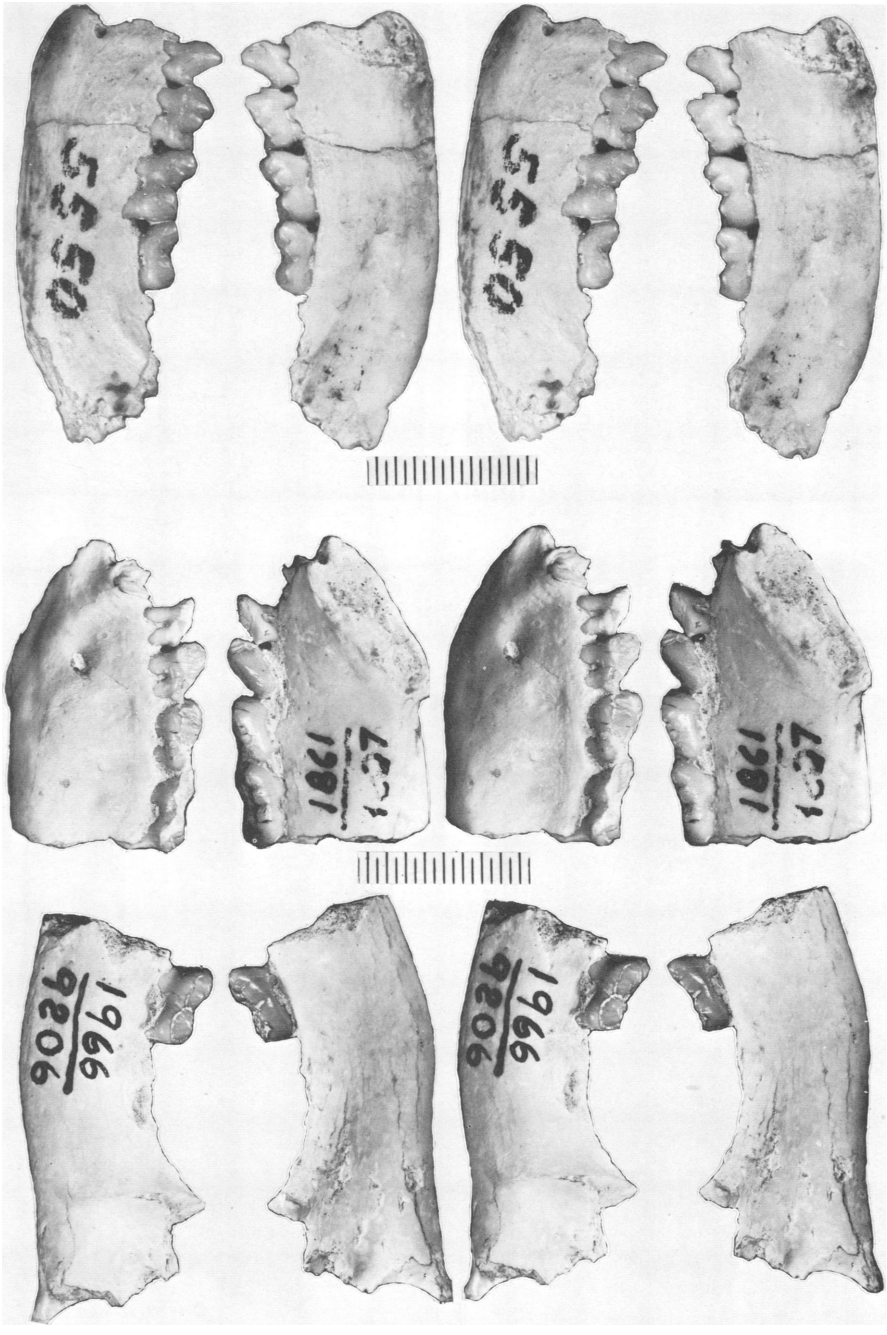


FIG. 130. *Ekgmowechashala philotau*, SDSM 5550, type, left mandible fragment with P_3-M_2 (above); LACM 9207, left mandible fragment with P_2-M_1 (middle); and LACM 9206, left mandible fragment with M_2 (below); all from Sharps beds. Stereophotographs: lateral (left) and medial (right) views, respectively. Subdivisions on scale represent 0.5 mm.

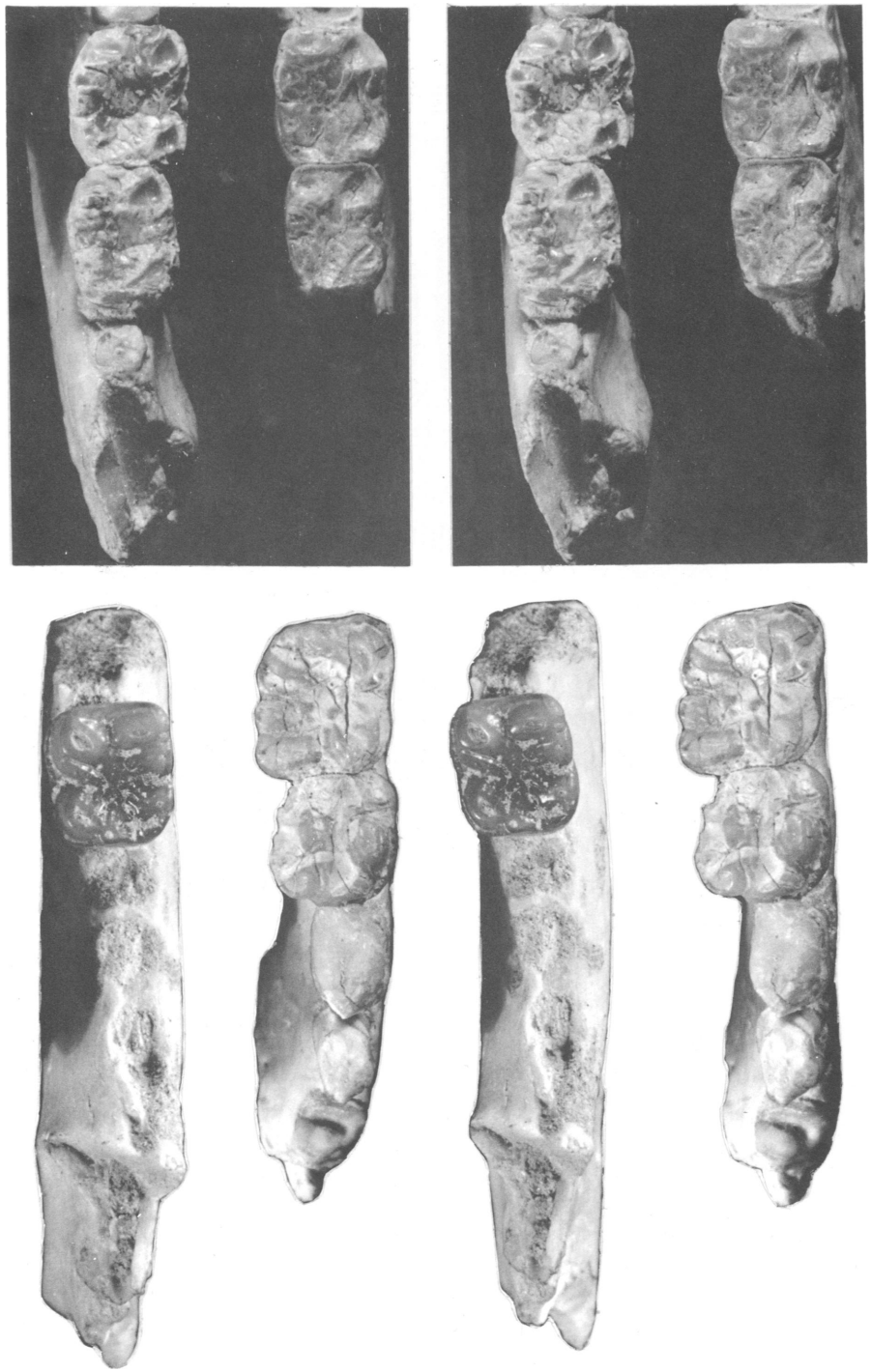


FIG. 131. *Ekgmowechashala philotau*, SDSM 6247, right M_{1-2} (above left); SDSM 6242, right M_{1-2} (above right); LACM 9207, left P_2-M_2 (below left); and LACM 9206, left M_1 (below right); all from Sharps beds. Stereophotographs: occlusal views.

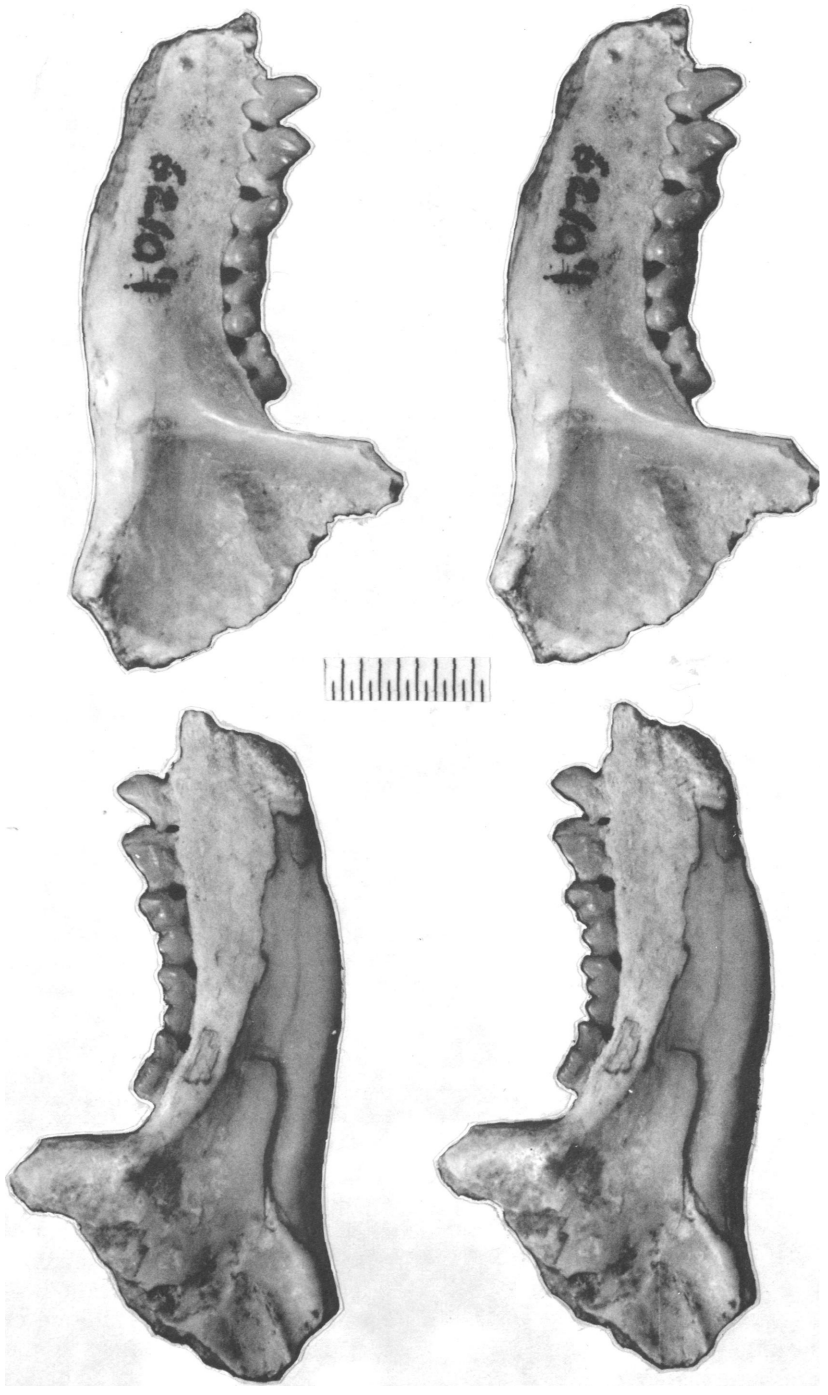


FIG. 132. *Ekgmowechashala philotau*, SDSM 62104, Sharps beds, left P_3-M_3. Stereophotographs: above lateral and below medial views. Subdivisions on scale represent 0.5 mm.

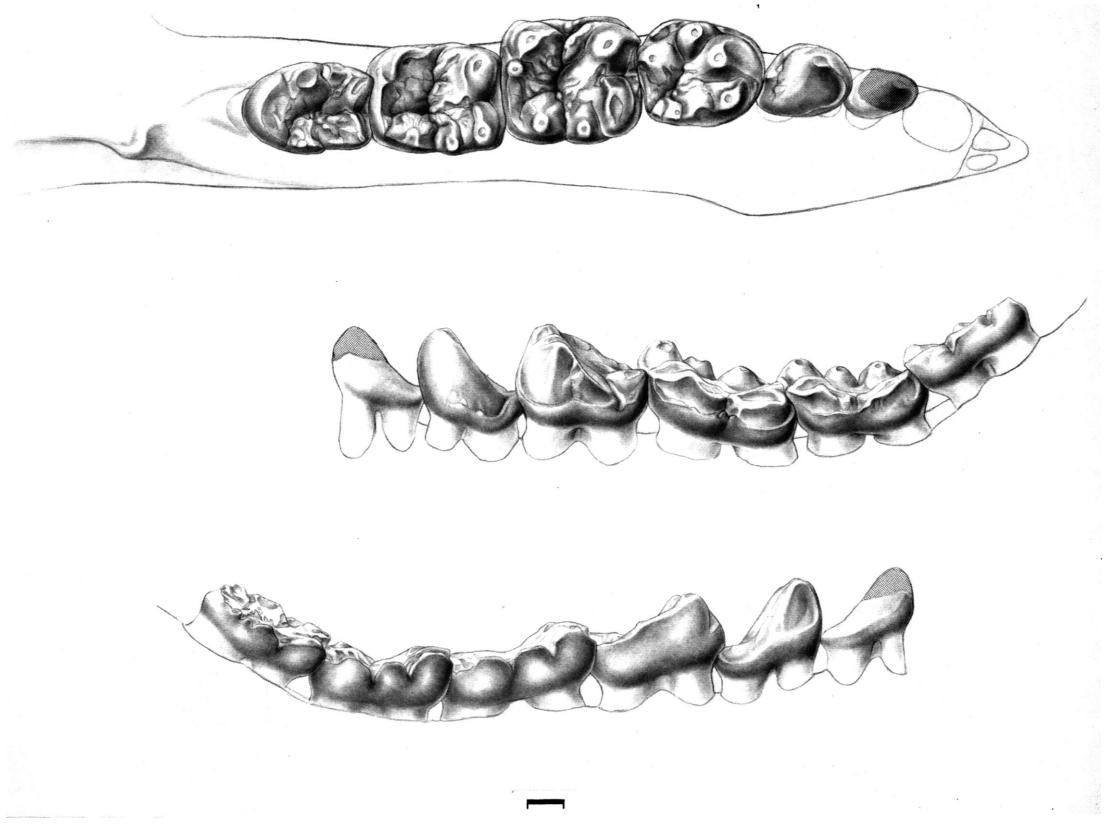


FIG. 133. *Ekgmowechashala philotau*, left lower dentition, alveoli for I_{1-2} and C, and P_3-M_3, based on SDSM 5550 and 62104 and LACM 9207, early Arikareean of South Dakota and Oregon; occlusal (above), buccal (middle), and lingual (below) views, respectively. Reconstruction shown by uniform stippling. Scale represents 1 mm.

Type Species. Teilhardina? gallica Russell, Louis, and Savage, 1967.

Included Species. The type species only.

Geographical and Temporal Distribution. Sparnacian (early Eocene) of France.

Generic Diagnosis. Donrussellia differs from *Teilhardina* in the following features: P_4 is transversely less wide; the basal part of the trigonid cusps, particularly the metaconids, is less inflated; the third molars are relatively larger; the upper premolar, MNHN 4711, shown in figures 135 and 136 (either P^3 or P^4), is relatively longer mesiodistally than either P^3 or P^4 of *Teilhardina*; the molars are less transverse; the metaconule on known molars is not clearly defined, being part of the postprotocrista, and the M_3 talonids, unlike those of *Teilhardina*, are not reduced.

Discussion. When describing the type species, Russell, Louis, and Savage recognized that eventual generic separation of this species from *Teilhardina* might become necessary. The remarkable aspect of this new genus lies in what I suspect to be its "intermediate," i.e., nearly equally similar, nature to an omomyid and adapid morphotype. Studying the known evidence I find it impossible to decide, based both on overall similarity and on sharing of a variety of subtle specializations, whether this taxon is more recently related to *Teilhardina* or other omomyids on the one hand, or to the common ancestors of *Pronycticebus*, *Anchomomys*, *Proto-*

FIG. 134. *Ekgmowechashala philotau*, partial left mandible with P_2-M_3, based primarily on SDSM 62104 and LACM 9207, early Arikareean of South Dakota and Oregon; lateral (above) and medial (below) views, respectively. Scale represents 1 cm.

adapis, and *Pelycodus* on the other. Because the very real possibility exists that *Donrussellia* does share a more recent common ancestor with the omomyids than with adapids and because it does in fact represent the most primitive known dental morphology for the Omomyidae, the new genus is described in this monograph. Recovery of anterior teeth and postcranials in association with the cheek teeth will undoubtedly shed light on the affinities of this important genus.

Adaptations. This taxon has low-crowned, somewhat squared molars with low conules combined with relatively high-cusped premolars.

The best guess at this time about the relatively

TABLE 27
Numerical Data for All Known Specimens of *Ekgmowechashala philotau*

	N	OR	R	M±SE	SD±SE	CV±SE	SK	KS
P^4								
L	1	3.45	–	–	–	–	–	–
AW	1	4.12	–	–	–	–	–	–
L/AW	1	0.84	–	–	–	–	–	–
M^1								
L	1	3.65	–	–	–	–	–	–
AW	1	5.20	–	–	–	–	–	–
L/AW	1	0.70	–	–	–	–	–	–
P_2								
L	1	2.61	–	–	–	–	–	–
PW	1	1.70	–	–	–	–	–	–
L/PW	1	1.54	–	–	–	–	–	–
P_3								
L	3	2.48-3.45	–	2.960±0.280	0.485±0.198	17.753±7.248	–	–
PW	3	2.00-2.20	0.875	2.067±0.067	0.115±0.047	6.053±2.471	–	–
L/PW	3	1.24-1.57	–	1.428±0.098	0.169±0.069	12.833±5.239	–	–
P_4								
L	3	3.50-3.78	–	3.660±0.083	0.144±0.059	4.269±1.743	–	–
PW	3	2.80-3.22	−0.178	3.070±0.135	0.234±0.096	8.268±3.375	–	–
L/PW	3	1.10-1.32	–	1.198±0.066	0.114±0.047	10.311±4.209	–	–
M_1								
L	3	3.73-4.63	–	4.153±0.261	0.452±0.185	11.799±4.817	–	–
PW	3	3.50-3.87	0.956	3.640±0.116	0.201±0.082	5.975±2.439	–	–
AW	3	3.65-3.74	0.913	3.680±0.030	0.052±0.021	1.530±0.624	–	–
L/PW	3	1.07-1.20	–	1.139±0.039	0.067±0.027	6.351±2.593	–	–
M_2								
L	3	3.70-4.32	–	3.923±0.199	0.344±0.141	9.511±3.883	–	–
PW	3	2.95-3.43	1.000	3.123±0.154	0.266±0.109	9.238±3.771	–	–
AW	3	3.10-3.42	0.997	3.207±0.107	0.185±0.075	6.242±2.548	–	–
L/PW	3	1.25-1.26	–	1.256±0.002	0.003±0.001	0.262±0.107	–	–
M_3								
L	2	3.60-4.05	–	–	–	–	–	–
PW	2	2.45-2.58	–	–	–	–	–	–
AW	2	2.35-2.50	–	–	–	–	–	–
L/PW	2	1.47-1.57	–	–	–	–	–	–

poor sample is that it belonged to an animal which was insectivorous, subsisting on insects and some fruits. There are no outstanding specializations in the known material which warrant postulation of any particular type of herbivory.

Etymology. For Dr. Donald E. Russell, in recognition of his outstanding studies on early Tertiary mammals.

Donrussellia gallica (Russell, Louis, and Savage, 1967), new combination
Figures 135-137

Teilhardina? gallica Russell, Louis, and Savage, 1967, p. 5.

Type. MNHN Av 5755, left M_2, collected from Avenay Quarry, France.

Hypodigm. The type and MNHN Av 4562,

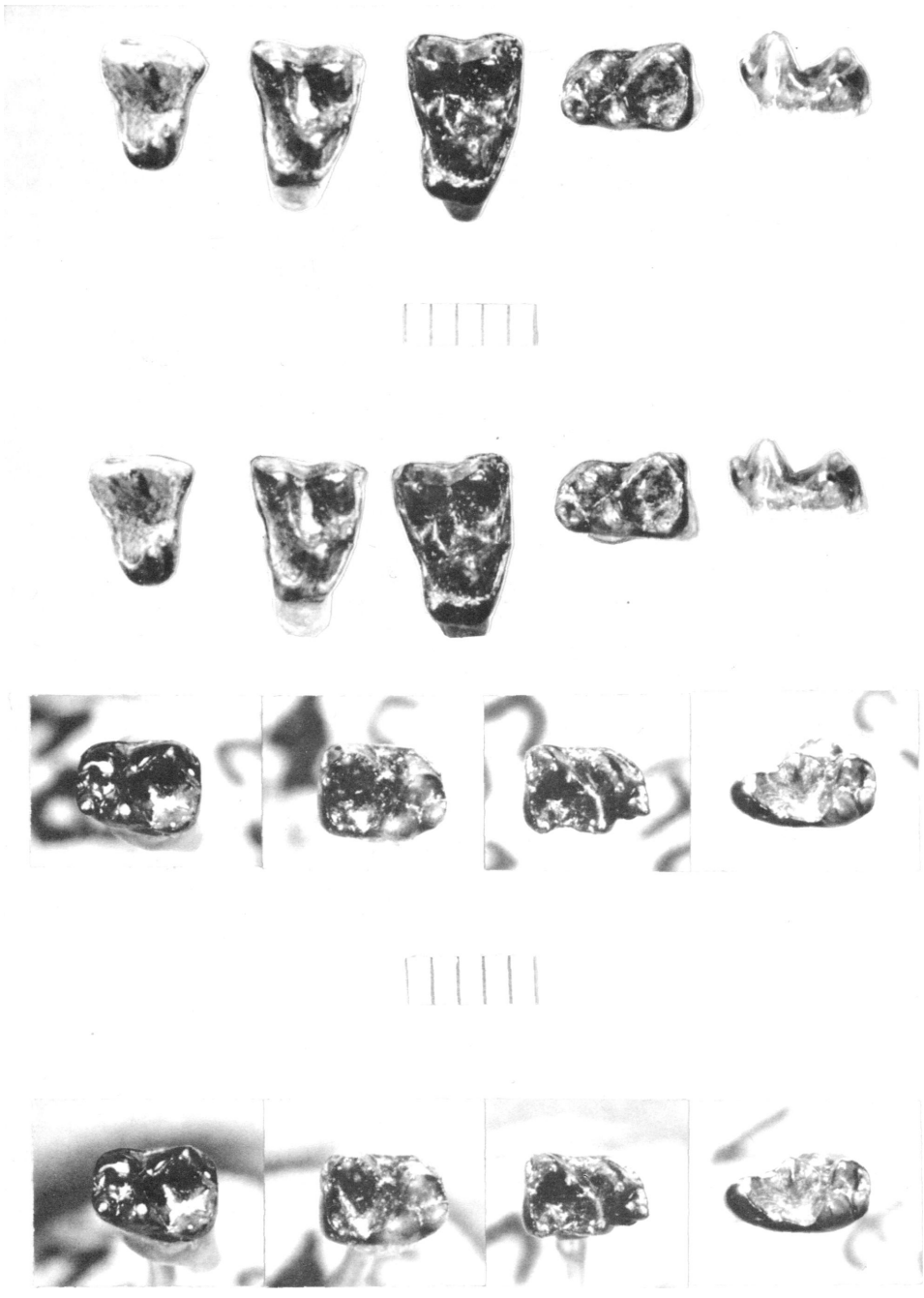


FIG. 135. *Donrussellia gallica*, top from left to right: MNHN Av 4711, right P^4 or P^3; MNHN 4855, right M^1; MNHN Av 5767, right M^2; MNHN Av 5873, right M_1; MNHN Av 4603, right M_2; bottom from left to right: MNHN Av 4562, right M_2; MNHN Av 5755, type, left M_2; MNHN Av 5017, left M_1; and MNHN Av 5721, left M_3; all from Avenay Quarry. Stereophotographs: all occlusal views, except MNHN Av 4603 which is in lingual views. Subdivisions on scales represent 0.5 mm.

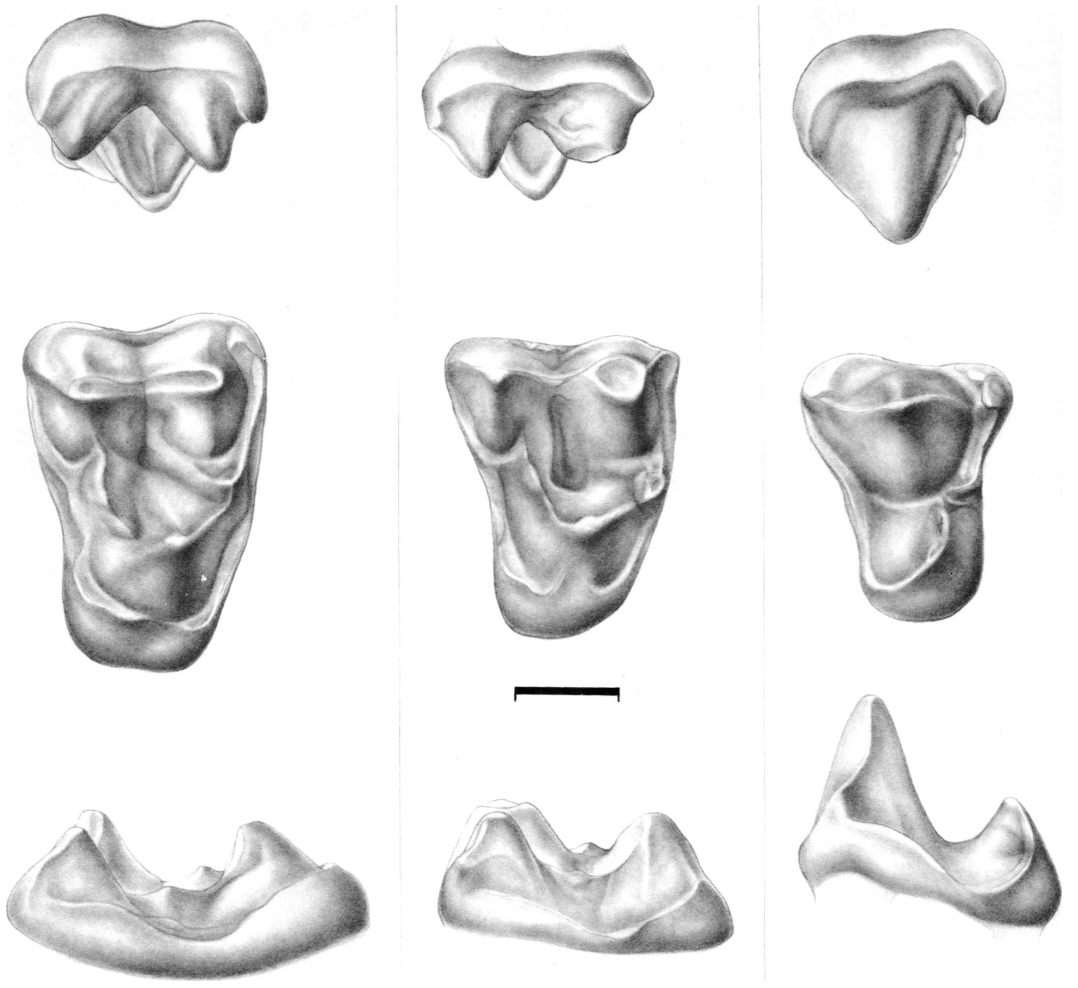


FIG. 136. *Donrussellia gallica*, from right to left: MNHN Av 4711, right P^4 or P^3; MNHN Av 4855, right M^1; MNHN Av 5767, right M^2; all Sparnacian of France; buccal (above), occlusal (middle), and distal (below) views. Scale represents 1 mm.

4603, 4711, 4855, 5017, 5721, 5767, 5873, all from Avenay Quarry.

Geographical and Temporal Distribution. Same as for the genus.

Specific Diagnosis. Only known species of the genus.

Genera Excluded from the Omomyidae

Agreement has been surprisingly widespread as to what genera should belong in the Omomyidae *sensu stricto* or the Omomyinae of previous authors. Nevertheless, several taxa have been disputed, particularly those from Europe and Asia. I will briefly review the status of those I do not consider to be omomyid, or those unlikely to be tarsiiform.

Navajovius Matthew and Granger, 1921, was treated in some detail in 1969 (Szalay, 1969a, pp. 275-281). At that time I suggested that *Navajovius* was a ?microsyopid, but subsequently (Szalay, 1972b, p. 9) I was convinced of the

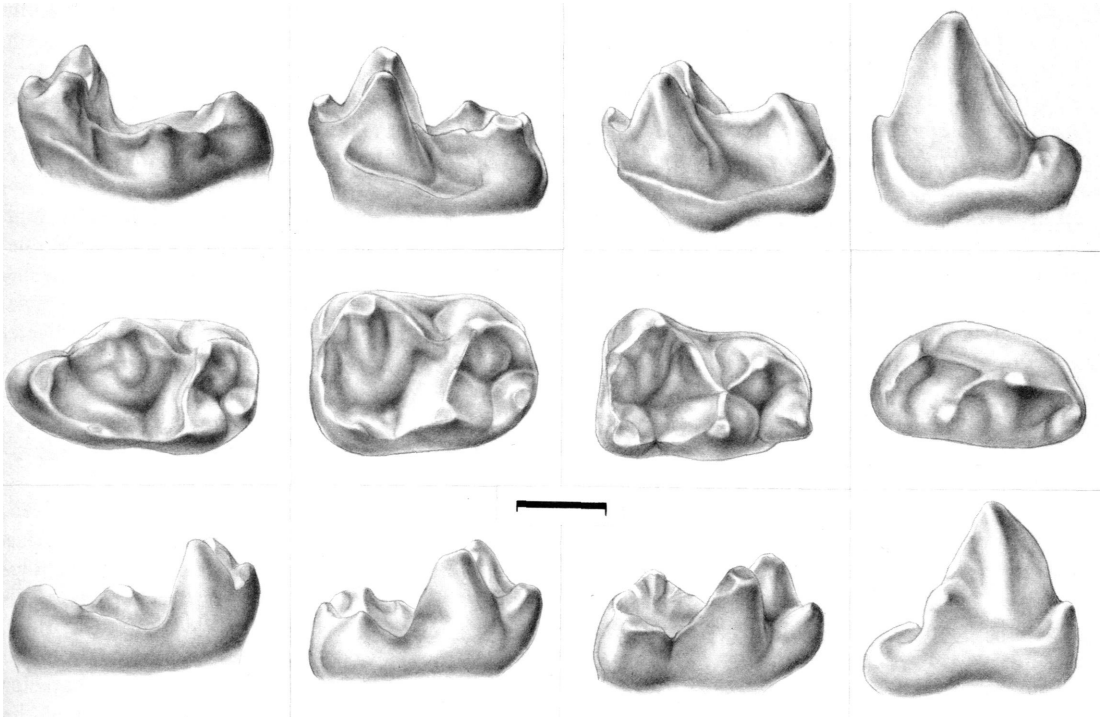


FIG. 137. *Donrussellia gallica*, from right to left: MNHN Av 5795, left P_4; MNHN Av 5017, left M_1; MNHN Av 5755, left M_2; and MNHN Av 5721, left M_3; all Sparnacian of France; buccal (above), occlusal (middle), and lingual (below) views. Scale represents 1mm.

paromomyid ties of the genus. Russell, Louis, and Savage have suggested (1967, fig. 14) that *Navajovius* is an omomyine. Since my 1969 study my conviction that *Navajovius* is not an omomyid or that it is not anywhere near the ancestry of that family has grown. The specialized premolars, particularly the highly modified P^3 completely lacking a protocone, are one of the strongest arguments that may be used to bar this genus from a structurally ancestral position either for the Paromomyidae or the Omomyidae. Illustrations of this genus are to be found in Szalay (1969a, pls. 30, 31).

Berruvius Russell, 1964, a poorly known primate of the French late Paleocene and early Eocene, was suggested by Russell, Louis, and Savage (1967) to be an anaptomorphine. The relatively small M_3, small in a manner different than M_3s of most anaptomorphines, and the trigonid suggest to me that this genus is unlikely to be an omomyid. *Berruvius* in fact may be considered as a European close relative of *Navajovius* on the basis of the fragmentary evidence (*contra* Szalay, 1969a).

In 1962 (p. 32) Simons classified the European early Eocene *Cantius* and the European medial Eocene *Periconodon* in the Omomyidae. In 1963 (p. 67) in addition to these he included *Hoanghonius* and *Lushius*, both from the Eocene of China, and classified *Niptomomys* in the Omomyidae and *Uintasorex* in the Anaptomorphidae, following McKenna (1960) and Gazin (1958), respectively. All of these, except *Cantius* were also listed in the Omomyidae of McKenna's 1967 classification of the prosimians.

Russell, Louis, and Savage have exhaustively argued that *Cantius eppsi* is really *Pelycodus eppsi* and this latter is clearly an adapid. These same authors have also argued against Simons's (1962) views on *Periconodon*, showing why it is

an adapid and not an omomyid. I have studied *Periconodon* in Basel in 1968 and in 1972 and I conclude that the adapid ties of this genus are doubtless. The similarities of the molars to *Anchomomys*, *Microadapis*, *Protoadapis*, *Leptadapis*, and *Adapis* are compelling in spite of pericone development in *Periconodon*, which is, incidentally, better developed in the genus *Lemur* than in *Omomys*. I have elsewhere (Szalay, 1969b) discussed the affinities of *Niptomomys* and *Uintasorex*, both of which I considered to be a closely related group of the nonprimate family Microsyopidae.[1]

I have closely examined the specimens from the medial Eocene Geiseltal brown coals on which Weigelt (1933) based the alleged primate taxa *Ceciliolemur* and *Microtarsioides*. I judge both of these taxa to have been based on very young specimens of metatherians, both probably of the same species of *Peratherium*.

As the known specimens of *Lushius* and *Hoanghonius* are presently not easily accessible (they are in China), no students other than the describers have had the opportunity to examine them. The published figures, however, indicate that these taxa are lemuriforms.

PHYLOGENY AND CLASSIFICATION

Evaluation of resemblances, results of which led to the conclusions on the phylogenetic relationship advocated in this monograph, was based mostly on the cladistic methodologies outlined by Hennig (1950, 1965, 1966). Hennig's central contribution, in which he distinguishes the relative merits of similarities between taxa for phyletics due to sharing of (a) primitive (ancestral, plesiomorph) features, (b) advanced (derived, apomorph) features, and (c) convergences, has profoundly influenced my analysis of homologous character states and subsequently my decisions on phylogeny. As most systematists know, single characters sometimes cannot be isolated but rather the total gestalt of given character complexes is judged on the basis of one of the three categories of resemblance. As advocated by Hennig, most recent relationships between two or more taxa are recognized on the basis of shared derived characters, synapomorphies, from a common ancestry, whereas shared primitive features, symplesiomorphies, between several taxa merely indicate that they all once shared a common ancestor.

Character states of the same feature of both fossil and living taxa may be arranged to form a morphocline (Maslin, 1952; Simpson, 1943; Schaeffer, Hecht, and Eldredge, 1972), which includes primitive to derived character states. Maslin called the inferred sequence the polarity of characters, and usually there are two widely used criteria to establish whether a character or its various conditions are primitive or advanced. If a feature widely occurs in a higher category it is often judged to be the ancestral condition, whereas the reverse, rare condition unless modified by unusual circumstances, is considered derived. Characters may be considered derived if their occurrence, according to the above criterion of exclusive presence in the taxa considered, correlates with other derived characters.

[1]The paper by Bown and Gingerich (1973), in which they wished to demonstrate that the Microsyopidae are primates, is unconvincing for two reasons. First, they chose to disregard the basicranial evidence available for the microsyopids and paromomyiforms, making no attempt to incorporate it into their final analysis. Second, they violated some basic rules of phylogenetic assessment by making their comparison of bona fide primates such as *Plesiolestes* not with the two oldest and (independently of age) most primitive of microsyopines, *Cynodontomys wilsoni* and *C. alfi*, but with the younger and more evolved *C. latidens*. Both McKenna (1960) and Szalay (1969a) show in specimens of *C. augustidents* and *C. wilsoni*, respectively, that the fourth premolars, associated with molars, are premolariform and not semimolariform as are those of the more derived *C. latidens*. Thus, Bown and Gingerich (1973) demonstrated that the similarities which exist between *Plesiolestes* and *Cynodontomys latidens* are convergent. They have, inadvertently, made the strong point that microsyopid similarities to the earliest primates are not due to common inheritance. Using their lines of reasoning and if we ignored the basicranial and pedal evidence, we would be obliged to reclassify several genera of undoubted artiodactyls with the primates on the basis of dental similarities to some genera of Eocene lemuriforms. This approach utilizes false parsimony. In favor of a hypothesis not falsified by one line of evidence, others, which falsify the theory, are ignored.

A lucid and thorough review on methods of phylogenetic inference has been provided by Schaeffer, Hecht, and Eldredge (1972). These authors reviewed the crucial concepts of homology vs. convergence and morphocline polarity (i.e., the estimation of what is primitive and what is advanced in a series of homologous characters) and advocated a mostly sound cladistic methodology, rooted in the contributions of both the school of evolutionary systematics as well as those of Hennig (1965, 1966) and other cladists. Yet I disagree with a rigid application of a purely cladistic methodology that advocates the unqualified rejection of the temporal and geographical attributes of fossils.

Schaeffer, Hecht, and Eldredge (1972) stated with great clarity what they believe the attitude of the paleontologist should be in regard to cladistic phylogenetics. They stated (p. 43), ". . . biostratigraphy is rarely relevant to the problem of working out relationships because it may add a distorting bias, and that identification of an actual fossil taxon with an ancestral morphotype is unnecessary for the delimitation of relationships." I believe that they have underrated the relative importance of the temporal dimensions of fossil taxa for phyletic studies. As Hennig's cladistic methodology advocated by them is an essentially workable one, I would like to briefly point out that the temporal position of some taxa in a study is perhaps not so often irrelevant as they suggest. Most paleontologists would probably agree that exact common ancestors in the fossil record on the species level may be rarities. A cladistic analysis of all taxa (fossil and extant) can yield morphotypes, however, of which one can state with sufficient probability that they are more nearly related to known species of one as opposed to other known fossil taxa. The results are usually a phylogenetic hypothesis, clearly more useful and closer to reality than the perhaps unduly pessimistic view that it is impossible to find common ancestors.

Today the full appreciation of paleogeography via plate tectonics and paleozoogeography as revealed by the fossil record are coming into their own for systematic biology. The necessity of estimating whether corridors, barriers, filter bridges, sweepstakes routes, Noah's arks, and beached Viking funeral ships [the first four Simpson's and the last two McKenna's (1973) concepts] existed between moving land masses at a given time is perhaps more important than ever. Thus, the spatial and temporal position of the fossil taxa add a crucial dimension to the analysis of their morphology. Often polarity cannot be inferred with clarity, and equally often the geographical information adds the required character to a given taxon which makes it useful in the construction of a theory of relationships.

In conclusion then, biostratigraphical, i.e., temporal and ecological information is as much a part of the evolutionary biology of taxa as their more tangible phenotypic attributes. In addition, the time dimension supplied by those fossils which either are, or closely resemble, a morphotype allows the only tangible approximations of the actual phylogeny of a group, rather than having the necessarily less sophisticated assessments offered by cladograms when time dimension is either not available or ignored. Thus, the fossil record, obviously only for groups that have one, will continue to render its special attributes for phylogenetic analyses, the very nature of which is biological history; the fossils are the signposts of this history. It is perhaps no accident that, by the standards of the most stringent character analysis, *Hyracotherium* (Paleocene and Eocene) is the most primitive perissodactyl, whereas *Equus* (Recent) is one of the most derived ones. The oldest genera of this monographic study, *Teilhardina* and *Anemorhysis*, are among the most primitive of omomyids and *Ekgmowechashala*, the most derived one, is the youngest. Mammalian paleontology, admittedly with the best record among the vertebrates, abounds with examples like these. It is obvious, but apparently worthwhile stating, that only the fossil record offers the answer to questions of the "whens" and "wheres" of evolutionary inquiries, problems often tied to genealogical questions.

There is no mention by Schaeffer, Hecht, and Eldredge (1972), in their assessment of phylogenetic analysis as conducted by paleontologists, of the use of functional studies in systematics and it is perhaps silently implied or the supposition is allowed that the polarity of characters and homologies can be satisfactorily discovered in order to infer phylogeny. It is often said by systematists that the reliability of their phylogenetic hypothesis is largely dependent on the diversity and abundance of usable

characters. It is also often said of the fossil record or of living forms of some groups that these are not adequate bases for phylogenetic inferences of even gross levels of resolution. As perhaps all biologists who have conducted some functional research into the meaning of character complexes could testify, studying mechanical function in both fossil and living taxa and the biological role of these character complexes in living forms yields surprisingly great "numbers" of new characters or new, more profound appreciation of "known" ones. This increase in the available and analyzable fossil and neontological information allows an often more convincing arrangement of morphocline polarity and more clearly established homologies (including homologous functions, *fide* Bock, 1969, p. 72) and hence often permits construction of more reliable phylogenetic hypotheses where usually the evidence, prior to a functional study, was judged to be inadequate. Yet, as functional anatomical studies often ignore the polarity of characters studied and thus deprive the work of the phyletic meaning of the very functional explanations they seek, similarly systematic studies can greatly weaken their analyses of character states when functional considerations are set aside.

Search for improved phylogenies should not stop, and the multidimensional nature of phylogeny should not be jammed into a tabulated system which should be as much of a guide to anagenesis as to cladogenesis–a necessary compromise (*fide* Simpson, 1961, and Mayr, 1969). Ultimately causal explanations rooted in natural history are sought to explain divergent morphologies of related taxa. A classification, therefore, should reflect adaptational as well as phylogenetic information (essentially as outlined by Simpson, 1961). I believe, as do most other evolutionary systematists, that classification based entirely on phylogeny, ignoring phenetic diversity (as advocated by Hennig and the other pure cladists), takes away the biological meaning of classifications. The somewhat robot-like construction of classifications every time the recognition of new character states or reinterpretation of known ones forces minor adjustments in the recency of relationships could cause chaos in a short time. Hennig's methodology as to the actual construction of classifications, based exclusively on a rigid system following phylogeny alone, is then not followed. A classification which is based exclusively on the inferred phylogeny of taxa is more apt to change as new data force the re-evaluation of phylogenetic hypotheses. The classification presented here (see table 29 and the Contents) is based on both phylogeny (still poorly understood!) and the degree of divergence of morphology.

It should be emphasized that although most evolutionary systematists (myself included) reject the classificatory practices proposed by the pure cladists that would require phylogeny as the sole criterion for a classification, they usually accept a definition of monophyly whereby a monophyletic group is defined to contain the most recent common ancestor of all the descendants included in that group. This does not mean, however, as pure cladists would have it, that all descendants of that common ancestor must be included in that group (see Ashlock, 1972, in particular).

Much of the literature concerning the nature of resemblances and differences between omomyid taxa, including the present study, should be read with caution. In the case of a large number of noted resemblances between various taxa, decision could not be reached with sufficient probability as to whether the similarities represented ancestral character states of a higher category uniting the taxa compared or derived characters independently acquired or inherited from the most recent common ancestor. In particular, I keenly appreciated these difficulties when analyzing the molar patterns, morphological and functional entities of extreme complexity. Although dental traits are useful for taxonomic delineations, it can be an extremely difficult matter to decide whether one deals with symplesiomorphy, synapomorphy, or with convergent character states when judging crown morphology. New fossils are needed together with increasing knowledge of form-function and breakthroughs in the association of the latter with the crucial aspects of the dietary regime, such as hardness and texture of the food. There is no doubt that much of

the preliminary interpretations presented here will be considerably altered as these fields progress.

RELATIONSHIPS WITHIN THE OMOMYIDAE

In figure 138 I present the most plausible phylogeny I can infer for the known omomyid species. Almost all the evidence that entered into phyletic considerations within the family is dental in nature; therefore most decisions, whether character states were merely omomyid symplesiomorphies or synapomorphies between two or more species of the family, were based on the morphology of teeth. This is not an apologia for the use of teeth for phyletics but merely a commentary on their use. Omomyid dentitions, including cheek teeth, are extremely varied and this quality alone renders them useful in systematics. Of significance are the extreme complexity of mammalian molar crowns and the fact that relatively minor genetic changes affecting the dentition can greatly alter the gestalt of a tooth. As the whole tooth changes, however, the resulting new gestalt becomes difficult to analyze character by character state.

The relationships between species and genera are discussed under the respective tax above, and although the basicranial data of *Rooneyia* and *Necrolemur* would, strictly speaking, come under these headings they are more meaningfully discussed below.

RELATIONSHIPS OF THE OMOMYIDAE TO OTHER PRIMATES

I have relied heavily on some selected features of the basicrania, dentitions, and postcranial elements of known fossil and living primates, in varying order, to infer phylogeny. The features discussed range from "distinct" characters, such as the presence or absence of a vessel, position of a foramen, or the course of an artery, to those which can more meaningfully be described as character states or conditions. Whenever I characterize a character state for a given taxon it is always possible that a similar condition in another one might occur as part of its intrataxonal variation. Taking several distinct characters together (a complex of character states) to diagnose taxa, however, virtually eliminates the problems caused by convergence.

Cranial Morphology
Figures 139-148

Splanchnocranium. I found the available meager splanchnocranial information from omomyid crania to be relatively unimportant in assessing extrafamilial relationships.

Although the premaxilla is preserved in *Necrolemur*, unlike that in *Rooneyia* or *Tetonius*, the exact sutural contact between it and the maxilla is difficult to determine. In Montauban 9 (fig. 149), the best preserved cranium, or in any of the others, the premaxilla and maxilla appear to have fused very early in ontogeny, as this appears to be the case in *Tarsius*. The suture, in the position shown in the reconstruction by Stehlin (1916) and Simons and Russell (1960), cannot be verified, although it might well have been there at an earlier ontogenetic stage. As far as can be judged from the broken specimens the premaxilla was a large bone in both *Tetonius* and *Rooneyia*. The size of the premaxilla, again, cannot be judged; it cannot be said that it was relatively larger than in either *Adapis parisiensis* (Montauban 7) or *Leptadapis magnus* (Montauban 1).

In *Necrolemur* and *Tarsius* the large lacrimal is widely separated from the jugal by the maxilla. As this is not the case in *Rooneyia*, in which the two bones are practically touching, nor in *Adapis parisiensis*, *Leptadapis*, and *Pronycticebus gaudryi* where the jugal and the maxilla are in contact, this character appears to be correlated with relative size of the orbit rather than with any particular set of other characters. Unlike *Necrolemur*, but like the adapids listed, *Rooneyia* is a form with not excessively enlarged orbits. Thus, the degree of proximity of the lacrimal and jugal should not be considered too significant a taxonomic character.

As in *Necrolemur*, there is no os planum (the ethmoid component of the orbits, when visible) exposed in *Rooneyia*. The exposure of the eth-

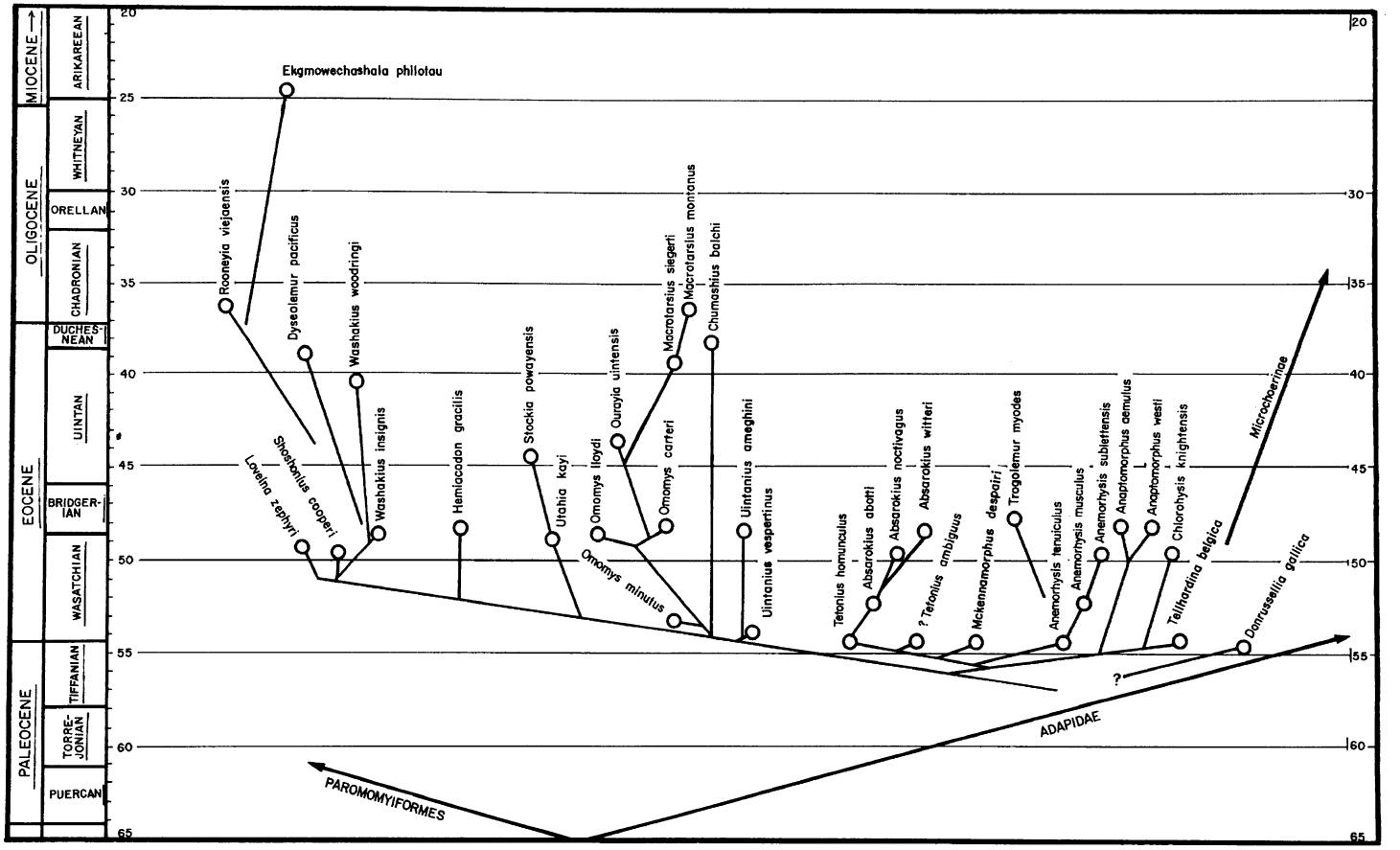


FIG. 138. Inferred relative, and estimated absolute recency of relationships of species included in the Anaptomorphinae, Omomyinae, and Ekgmowechashalinae.

moid in the orbits, as detailed by Simons and Russell (1960, p. 9), appears to be strongly correlated with the compromise of the orbital area to accommodate relatively large eyes as in *Tarsius* and in the large-eyed lorisids.

The large lacrimal foramina of the known omomyids are outside of the orbit as in *Plesiadapis tricuspidens*, *Pronycticebus* (see Russell, 1964), and *Notharctus*, but unlike in *Adapis parisiensis* and *Leptadapis magnus* which have this foramen just inside of the anterior orbital rim. As noted by Simons (1962, p. 17), specimens of *L. magnus* (PU 11481) are known in which the lacrimal foramen is outside of the orbit.

In the orbit of *Rooneyia*, as in *Necrolemur*, the maxilla is broadly in contact with the frontal, excluding the palatine from contacting the lacrimal. This condition is unlike that found in *Adapis parisiensis* and *Leptadapis magnus*, which have a broad palatine-lacrimal contact, excluding the maxilla from contacting the frontal. In the adapid *Pronycticebus*, however, the maxilla and frontal broadly contact excluding the palatine from the anterior part of the orbit.

The infraorbital foramen is small both in *Rooneyia* and *Necrolemur*, and in *Tetonius* it is double rather than single.

Endocasts. As with the features of the splanchnocranium, the known endocasts have not been very important in the phyletic studies of tarsiiforms.

The endocranial casts of *Tetonius*, *Necrolemur*, and *Rooneyia* were recently treated by Hofer (1962), Hofer and Wilson (1967), and Radinsky (1967, 1970). The endocranial cast of *Tetonius homunculus* was described in detail by Radinsky (1967) who pointed out the relatively large olfactory bulbs and the small frontal lobes, likely to be ancestral haplorhine or primate features. He also called attention to the relatively large occipital and temporal lobes, as well as to the slightly overlapped cerebella, which are probably advanced primate characters. The similarity of the endocast morphology of *Necrolemur* to *Tetonius* is striking, and this is likely to be a synapomorphy.

The most notable feature of the endocast of *Rooneyia*, as cited by Hofer and Wilson (1967) and by Radinsky (1970), is its lack of sulci other than the Sylvian. The coronolateral sulcus is absent in *Rooneyia*, as in the other omomyids, and was present in the adapids *Smilodectes* and *Adapis* (Radinsky, 1970, pp. 220-221). The absence of this sulcus may differentiate early tarsiiforms from adapids, in which it was apparently present. Obviously, a certain absolute size is necessary for this sulcus to be noticeable. Thus, for example, probably because of its small size, the endocast of the extant *Microcebus murinus* lacks this sulcus although the larger lemurs clearly display it.

Basicranium. (Abbreviations on pp. 166-167.) The basicrania of mammals have proved to be of very great significance in assessing phyletic relationships above the generic level. There have been numerous detailed studies in the past (Gregory, 1920; van der Klaauw, 1931; Lamberton, 1941; Simons and Russell, 1960; Saban, 1963; and many others) dealing primarily with the bony orifices of this region of the cranium, but only a handful of works (Tandler, 1899; Saban, 1963; Bugge, 1972) attempted to identify the paths of various blood vessels and nerves in a comprehensive fashion. A large body of literature, primarily paramedical, exists on diverse circulatory patterns and anomalies of various "monkeys" and apes. As yet no synthetic works on primates exist in which attempts are made to causally explain all the basicranial skeletal morphology in relation to the function of the attached or traversing soft structures.

Most studies on the basicrania have dealt with adults of the species, a point of extreme importance in using the information in the literature. Future embryological studies of the basicranium for many of the known primates is a must to give credence to conclusions based on adult conditions.

There are relatively few well-preserved early Tertiary primate basicrania. The majority of the specimens, with the exception of those of adapids (Stehlin, 1912; Gregory, 1920; LeGros Clark, 1934), have been studied recently (Simons and Russell, 1960; Saban, 1963; Russell, 1964; Szalay, 1972a). Thus, in addition to a few undescribed petrosal bones from the Paleocene and Eocene the ear regions of the following early Tertiary primates are known: *Phenacolemur jepseni*, *Plesiadapis tricuspidens*, *Pronycticebus*

gaudryi, *Adapis parisiensis*, *Leptadapis magnus*, *Tetonius homunculus*, *Necrolemur antiquus*, and *Rooneyia viejaensis*.

I will now attempt to review and explore the phylogenetic significance of the basicranial evidence available not only for the known Omomyidae but also for the Paromomyiformes, Strepsirhini, and the Haplorhini in general. Without this overview the significance of various characters of the omomyids would be largely without phyletic and functional context.

The basicranial evidence from taxa of the Paromomyiformes is quite incomplete; only two genera, *Phenacolemur* and *Plesiadapis*, are known (figure 139). *Plesiadapis* has received detailed treatment by D. E. Russell (1964) and Saban (1963) but the relatively large number of known petrosals lead to contradictory interpretations in some areas of the middle ear. A new basicranium of *Plesiadapis tricuspidens* (Cartmill, personal commun.) clarifies previously unknown aspects of the genus. *Phenacolemur* has been recently described (Szalay, 1972).

A review of the evidence of *Phenacolemur* and *Plesiadapis* shows that the entry of the carotid into the bulla was posterior and the promontory artery was relatively very insignificant as, apparently, in all primitive Eutheria. A bony canal was probably present, at least for the portion of the internal carotid inside the bulla prior to the branching off of the stapedial. In *Phenacolemur* the canal appears to be continuous, but in *Plesiadapis tricuspidens* it only runs a short distance, as shown on figure 139. The fenestra rotunda appears to be obstructed in *Phenacolemur* when viewed ventrally. The ventrally shielded fenestra rotunda is a conspicuous feature of not only *Phenacolemur* but also of lemuriforms, and I suggest that this was also a diagnostic character of the primate morphotype. There is no appreciable petromastoid enlargement in either *Plesiadapis* or *Phenacolemur*, and in both genera the ectotympanic is partly extrabullar, although, significantly, to different degrees. This bone, although it is not ringlike in either genus, extends into the bulla in *Plesiadapis* and in both genera forms the base of the external auditory canal (Cartmill, personal commun.).

How can the differences in the conformation of the ectotympanics be explained in these two paromomyiforms, and which of these conditions is most likely to be primitive? As noted, the middle ear morphology of the two genera differ inasmuch as *Plesiadapis* has a large number of septae and in general a more inflated bulla. *Phenacolemur*, on the other hand, has only a longitudinal septum that houses the lateral carotid artery and its craniad continuation, the promontory artery. The great inflation of the bulla in *Plesiadapis* may supply the clue to the developmental events that led to the condition of the ectotympanic displayed by that genus. We may postulate an ancestral condition shown in figure 148C and view the development in *Plesiadapis* as the result of the lateral displacement of the petrosal during the general hypertrophy of the bulla itself. As in many other mammalian lineages, selection for increase in auditory sensitivity would have been accomplished by an increase in middle ear cavity volume. An extension of the middle ear cavity laterally, below the ear drum, would surround the medial end of the auditory meatus by the tympanic cavity, and thus make a large portion of the ectotympanic (true ectotympanic plus the ossified anulus membrane) intrabullar. Such a mechanism has, in fact, long been known in developing lemuriforms (Cartmill, personal commun.).

Phenacolemur, unlike *Plesiadapis*, apparently has no portion of its ectotympanic within the tympanic cavity, except for the crista tympani supporting the tympanic membrane. This condition, as that of *Plesiadapis*, may be slightly derived from that postulated in figure 148C. The probability is very likely therefore, that the extrabullar condition of *Phenacolemur* had been derived along pathways *analogous* (!) to those of *Tarsius* from an ancestor with an ectotympanic enclosed by the middle ear cavity.

In addition to the wealth of extant and subfossil species, fossil strepsirhines are reasonably well known cranially. Skulls or skull fragments of *Pelycodus*, *Notharctus*, *Smilodectes*, *Adapis*, *Leptadapis*, and *Pronycticebus* give a fair idea of cranial diversity. The two Miocene crania of lorisids, those of *Komba* and *Mioeuoticus*, suggest both a degree of anagenetic advance and at least an upper limit for the time of origin of lorisid skull morphologies.

It is possible that, in general, much of the

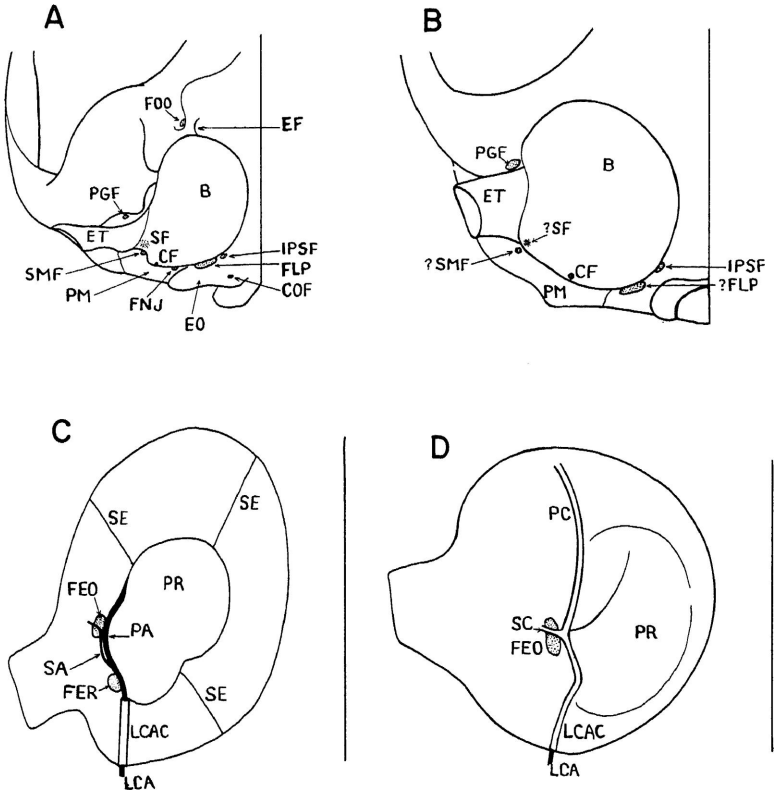


FIG. 139. Simplified schema of the basicranial morphology in known Paromomyiformes. A and C, *Plesiadapis tricuspidens* (late Paleocene), and B and D, *Phenacolemur jepseni* (early Eocene). Above: basicranium intact; below: the bulla and ectotympanic removed to show carotid circulation. For abbreviations see pages 166-167.

evidence we consider primitive lemuriform in both adapids and later lemuroids is largely primitive retention from paromomyiforms. I suspect that the intrabullar ectotympanic was part of the primate morphotype, but this judgment is very speculative as we lack adequate evidence from most paromomyiforms, erinaceotans, or other relevant early eutherians.

The only measure of the relative importance of blood transport in arteries of fossils is the relative size of the bony canals that housed them. Gregory's (1920) assertion about the differences in the relative sizes of the promontory and stapedial arteries in primitive strepsirhines and haplorhines was confirmed on new, and in the case of adapids, more primitive fossil material. I have drawn the diameters of the lateral internal carotid and the promontory and stapedial canals from AMNH 88802, a petrosal from the early Eocene East Alheit Pocket that I identify to be of *Pelycodus* sp., and from the Montauban 9 skull of *Necrolemur antiquus* from the ?late Eocene phosphorites of Quercy. Although the size of the promontory artery is by no means insignificant in *Pelycodus*, in the primitive notharctine the stapedial artery appears to have been the larger vessel immediately after the separation of the lateral internal carotid artery into the two former vessels. This is the condition overwhelmingly established for *Adapis*, *Leptadapis*, *Notharctus* (but see Gingerich, 1973), and extant Lemuridae (*sensu stricto*), Indriidae, and

Daubentoniidae. As stated by Gregory, *Necrolemur* and *Tetonius* clearly show the greater emphasis of the promontory as opposed to the stapedial canals, and therefore presumably of the arteries also. Thus the recognition of the early dichotomy between strepsirhine and haplorhine intrabullar circulations is perhaps justified.

The diversity of basicranial transformations among strepsirhines offers an excellent opportunity for character analysis. This fact, I believe, is of considerable significance for evaluating a variety of phylogenetic hypotheses, some recent, of both strepsirhine phylogeny and various aspects of strepsirhine evolution.

The diversified basicranial morphology of the strepsirhines (figs. 140, 141) offers evidence for a basically different hypothesis from that advocated by Martin (1972) and Groves (1972). This in turn is not significantly different from a scheme advocated by Gregory (1920), and appears compatible with other aspects of strepsirhine biology.

For purposes of this discussion there are three major basicranial categories among the strepsirhines. The adapids, lemurids, indriids, and daubentoniids share basic similarities, which can be described as those of a primitive lemuroid pattern. The Cheirogaleidae, the second group, are uniform in some of their distinctive characters. Similarly, the lorisids, the third group, are closely knit in sharing a number of clearly derived character states.

A review of strepsirhine basicrania indicates to me that the characters shown by the known

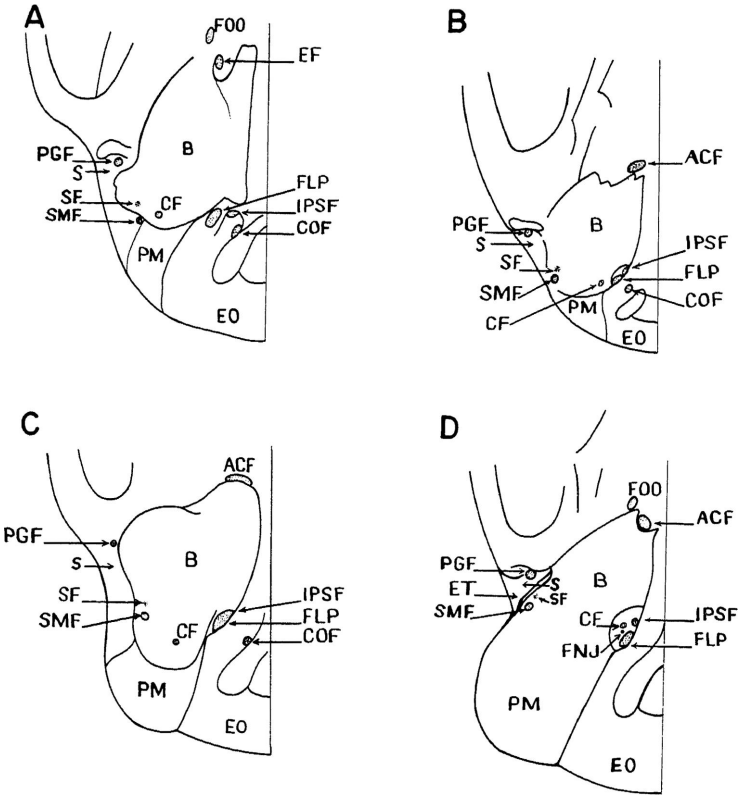


FIG. 140. Simplified schema of intact basicranial morphology of some representative Strepsirhini. A. *Lemur* sp. (Recent); B. *Microcebus murinus* (Recent); C. *Komba* sp. (early Miocene); and D. *Galago crassicaudatus* (Recent). For abbreviations see pages 166-167.

Adapidae, and to some degree by the Lemuridae, and Indriidae represent relatively unmodified versions of the primitive pattern for strepsirhines, although not necessarily for the order. Whenever we choose to determine polarity for any of the several characters found in two or more conditions, it is invariably the adapid-lemurid pattern that appears to be primitive, and the lorisid one derived. The cheirogaleids show an intermediate condition in some features although they possess some primitive and also some derived character states like those found in the lorisids. The most conspicuous advanced feature is the presence of an enlarged ascending pharyngeal artery (see Bugge, 1972) and an anterior carotid foramen in all forms here called lorisoids.

The following basicranial characters are particularly pertinent to this discussion of significant differences among the strepsirhines: (1) place of entry of the carotid and ascending pharyngeal arteries into the bulla; (2) absence or presence of an anterior carotid foramen and enlarged ascending pharyngeal artery; (3) relative size, or presence or absence, or the stapedial canal and artery; (4) relative size of the promontory canal and artery; (5) relative size of the petromastoid; and (6) relative size and position of the ectotympanic in relation to the petrosal.

Neither the details of the morphology nor some of the problems of function and homology surrounding them are discussed here. Lamberton's (1941) and Saban's (1956, 1963) contributions give exquisite detail of strepsirhine basicranial morphology, and Szalay and Katz (1973) recently discussed some issues of homology and morphocline polarity as they relate to strepsirhine phylogeny. The pertinent evidence and my interpretation of the homologies of vessels and openings in the basicrania are shown on figures 140, 141, and interpretations of the morphocline polarities are briefly stated below. As mere factual information, it is evident (see the figures) that (1) the entry of the internal carotid artery into the bulla is either central as in the Miocene cranium of ?*Komba*, KNMR 1005-50 or it is on the posteromedial side of the bulla as in extant genera; (2) the ascending pharyngeal artery of cheirogaleids and lorisids is not the promontory artery, as the latter is present in at least some stages of the ontogeny, coursing intrabullarly across the promontorium; (3) the petromastoid is greatly inflated in the extant lorisids; and (4) the stapedial circulation is insignificant in the lorisids in contrast with the lemuroids.

The basicranial evidence is therefore compelling in that it points to well understood morphocline polarities. As this is one of the better known and most diagnostic morphological complexes of strepsirhines, inasmuch as it clearly differentiates the major groups, I give it much weight in deciding their cladistic as well as anagenetic relationships. We may conclude, therefore, that the most ancient and ancestral strepsirhines were animals that can be characterized in terms of the known morphology of the adapids. Apart from the relatively larger brain and a tooth comb, the most recent common ancestor of the Lemuridae and Indriidae was either the most recent common ancestor of all the known tooth-combed strepsirhines or was, at least, more like a lemurid or indriid than a cheirogaleid or lorisid. The Cheirogaleidae were derived from a lemuroid, a form not unlike *Lepilemur*, or perhaps, but less likely, from a primitive indriid. The derived characters shared by cheirogaleids and lorisids, and the clear evidence of the entire skeleton favoring the primitiveness of the cheirogaleids compared with the lorisids indicate that a strepsirhine species of cheirogaleid affinity and of a similar level of organization was the ancestor of lorisids. I hold that the Lorisiformes, including both the Cheirogaleidae and Lorisidae, are derived descendants of much more primitive bona fide lemuroids, and most of the characters shared by all lorisiforms are advanced features not only among primates but also within the tooth-combed strepsirhines.

It is my working hypothesis that the common ancestor of known tarsiiforms was more recently related to the morphotype of the anthropoid primates than the latter to any other known groups of primates. I take the view, therefore, that it is heuristically justified to refer to the common ancestor of platyrrhines and catarrhines as having been derived from a tarsiiform.

It was Gregory (1915, pp. 430-431) who recognized the significance of the basicranium of *Tetonius* and stated that "The basicranial region, as a whole, is remarkably similar to that of *Tarsius* save that the trochlea, or auditory promi-

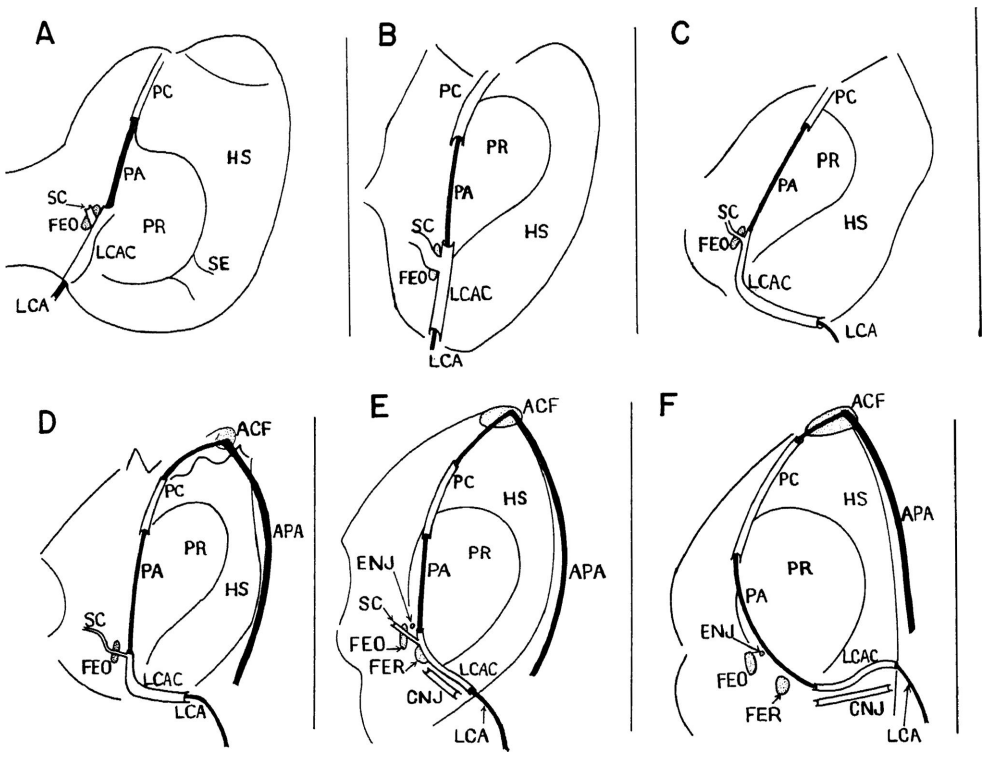


FIG. 141. Simplified schema of middle ear morphology and associated carotid circulation in A. *Adapis parisiensis* (medial or late Eocene); B. *Lemur* sp. (Recent); C. *Lepilemur* sp. (Recent); D. *Microcebus* sp. (Recent); E. Hypothetical condition based on the external morphology of *Komba* sp. (early Miocene); and F. *Galago crassicaudatus* (Recent). The bulla and ectotympanic are removed to show the carotid circulation. The various conditions depicted from A to F approximate the polarity of a morphocline for the character complex shown. For abbreviations see pages 166-167.

nence is much smaller. The bulla was greatly inflated, as in *Tarsius* and *Necrolemur*, and its anterointernal extension likewise completely covered over the region where the foramen lacerum medium is situated in the Nycticebidae [i.e., Lorisidae]. The internal carotid must surely have traversed the tympanic chamber, but its exact course is doubtful. In *Tarsius* it pierces the middle of the bulla on the lower surface, then passes directly upward (craniad) through the margin of the septum of the cavum bullae, passing into the cranial cavity at the apex of the enlarged cochlea (Kampen, 1905, p. 676). In the only known skull of *'Anaptomorphus' homunculus* the whole lower wall of the bulla is broken away, so the place of entry of the carotid into the cavum bullae is not indicated (figure 142). To the small cochlea is attached a remnant of a long septum, which may have carried the carotid canal." Further study of the specimen confirms Gregory's suggestion that the septum housed the promontory artery. This condition, then, is identical to that of *Necrolemur*. It is equally clear that virtually all other preserved details of the middle ear cavity in *Tetonius* match those of *Necrolemur*.

In all known paromomyiforms, most strepsirhines, and known haplorhines, the foramen lacerum posterior appears to be distinct from the usually smaller and more anterior inferior petrous sinus foramen. Clearly, this represents a shared primitive condition.

Tarsiiform basicrania containing varying amounts of information are known for *Tetonius*

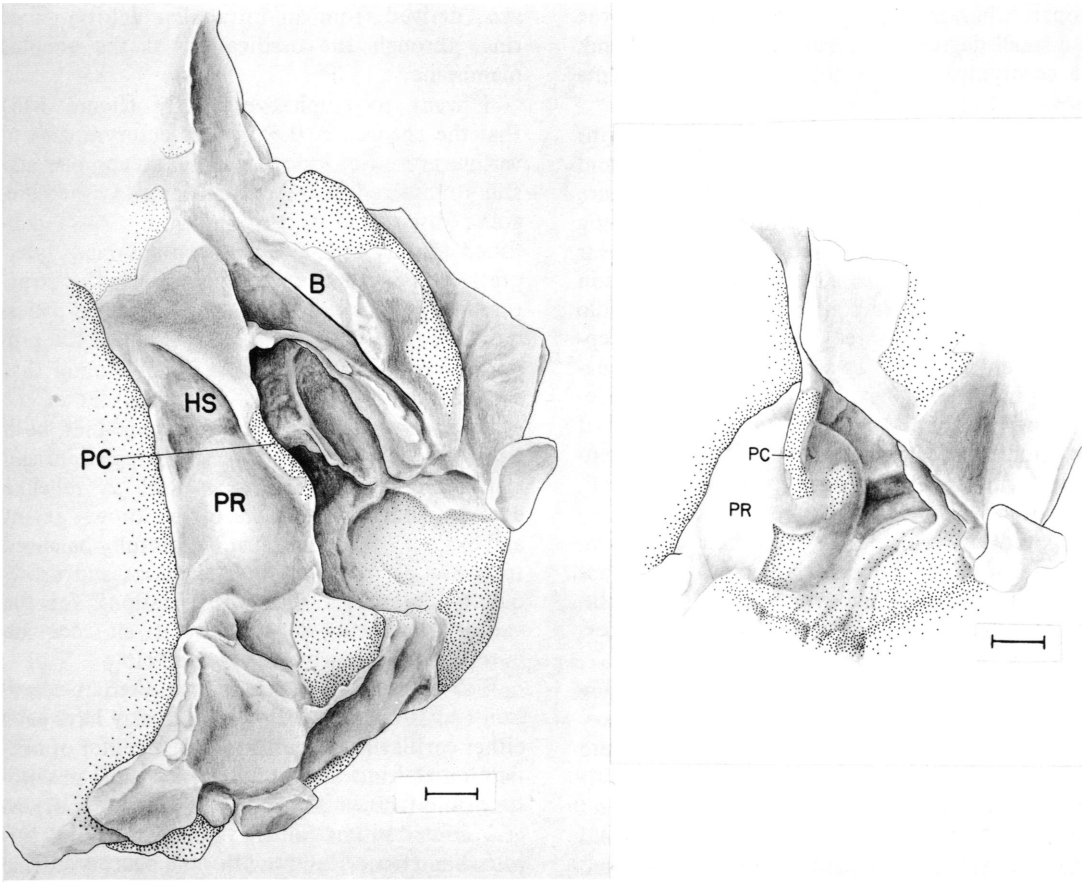


FIG. 142. Basicranium of *Tetonius homunculus*, AMNH 4194, Gray Bull beds. On left the view is ventral, whereas on the right only the middle ear cavity is shown in ventrolateral view. Scales represent 1 mm. For abbreviations see pages 166-167.

(figure 142), *Rooneyia* (figure 143), *Necrolemur* (figure 144), and *Tarsius* (figure 145). The sample is far from adequate and it appears sufficient only to allow assessment for a few characters that may diagnose the tarsiiform morphotype. Work is now in progress to further describe in detail the middle ear morphology of *Rooneyia* and up to now unrecognized aspects of *Necrolemur*. Cleaning of specimens of these taxa has revealed hitherto unknown characters of the middle ear and the ectotympanic.

When we view the middle ear cavity of the known tarsiiforms and compare them with specimens of adapids such as *Notharctus tenebrosus*, *Adapis parisiensis*, *Leptadapis magnus* or that of a new late Eocene adapid (Wilson and Szalay, in prep.), it becomes evident that a series of morphological stages, at least in a number of characters, are represented when we view them as a morphocline.

The most unique aspect of the middle ear morphology of *Rooneyia* is the presence of an ectotympanic deep within the tympanic cavity. This bone is continuous with a shelf, clearly an ossified annulus membrane, supported from below by two transversely long, stout struts. In *Necrolemur* a basically identical condition exists except that its ectotympanic is closely abutted against the bulla proper.

In *Rooneyia*, therefore, the middle ear cavity extends pervasively below the ossified annulus membrane and well lateral to the ectotympanic

proper, whereas in *Necrolemur* this is only true to a small degree. In *Tarsius*, on the other hand, the ectotympanic is in the most lateral extreme known within tarsiiform bullae.

Rather than only viewing the three tarsiiforms as representing three phylogenetic stages and thus as an aid in gaining an approximate picture of the phylogeny of this structure, the remaining characteristic morphologies of these middle ear cavities supply a partial adaptational explanation for the ectotympanic conformation. The middle ear cavities of all three tarsiiforms are exceptionally enlarged, yet in a divergent manner, suggesting independent evolution. As selection independently favored an increased relative size of the middle ear cavity for increased auditory sensitivity, divergent pathways were emphasized, perhaps as a result of different base (heritage) morphologies available for these taxa. *Rooneyia* extended the tympanic cavity below and lateral to the ectotympanic, *Necrolemur* enormously inflated the petromastoid, whereas *Tarsius* hypertrophied the hypotympanic sinus.

The point of entry of the carotid into the bulla is coupled with the enlargement of the promontory artery in known tarsiiforms (figure 146). The medial entry of the internal carotid is a primitive condition for the tarsiiforms and haplorhines, but it is derived when compared with the primitive strepsirhine and primate conditions. The path of the lateral internal carotid artery in *Tarsius* is clearly a more advanced version of what is seen in *Rooneyia*, *Necrolemur*, and *Tetonius*. In all these forms the promontory artery is relatively very large and relatively much more important than in any known strepsirhines. The comparative dimensions of the promontory and stapedial arteries in some fossils have been noted above.

The known omomyid basicrania, when integrated with postcranial evidence, suggest that the major characters which may be considered derived, having diverged after their origin from a primitive ancestral condition that can best be called lemuriform, were (a) increase in the relative size of the promontory artery compared with the stapedial artery; (b) medial shift in the entry of the carotid artery into the bulla; and (c) an increasingly extrabullar position of the ectotympanic, particularly as epitomized in *Tarsius*, derived from an intrabullar ectotympanic ring, through the ossification of the annulus membrane.

I want to emphasize briefly (figure 148) that the changes in the primate ectotympanic in various groups of the order present a complex and still unresolved series of problems, as the foregoing discussions should indicate. I have published (Szalay, 1972) a rather preliminary interpretive scheme to explain diversity in this structure within the order, but new facts and assessments require modifications of some of the proposed hypotheses. One must bear in mind that each of the three subordinal categories of the order have various types of ectotympanics, both narrow and wide, and both the Strepsirhini and Haplorhini have ringlike as well as tubelike ectotympanics. Knowledge of the known extant and extinct conditions must be carefully balanced to arrive at morphotype conditions and subsequent hypotheses of transformations for the various taxa considered even if an adequate developmental mechanism is available.

The hypothetical primitive eutherian condition (A) is one in which the bulla may have been either cartilaginous, perhaps with a center of ossification at some stage of the ontogeny, an entotympanic (rostral or caudal), or with one or several contributions to the bulla from the surrounding bones and with the ectotympanic partly lateral to the cartilage or bone. The configuration shown in A, which is not necessarily the immediate ancestral condition to B, is a remote structural stage. In B the petrosal is continuous with an ossified bulla, with the ectotympanic largely lateral to and in articulation with a petrosal bulla. This condition may or may not represent the primate morphotype.

As noted, derivation of the tarsiiform condition(s) is from a bona fide lemuriform. The sequence from a primitive tarsiiform (H) and from the latter to I and then to J is most probable. The morphotypes of the living cercopithecids and hominoids may have independently reached stage K from J. The strepsirhine and primate morphotype pattern is judged to be that shown in C, as exemplified by most lemuroids, and is most likely to have given rise to E, one of the lorisid condition. The analysis of the lorisid basicranium compels me to view the extrabullar

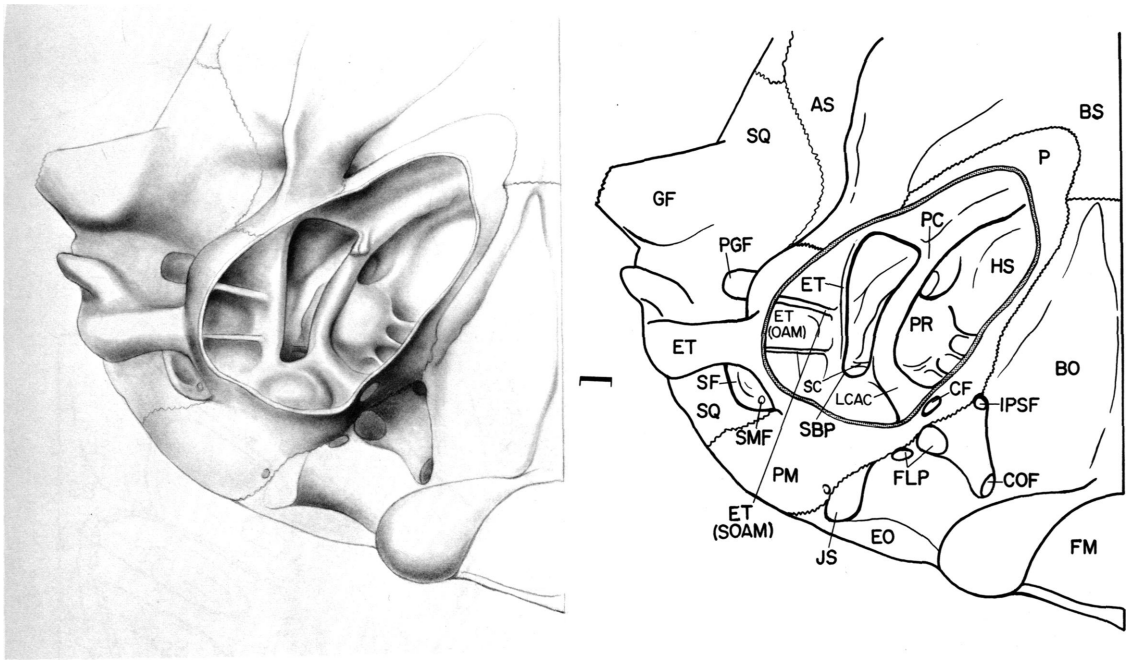


FIG. 143. Basicranial morphology of *Rooneyia viejaensis* with only the ventral floor of the bulla removed. Drawing is based on UT 40688-7. Ventral and slightly medial view. Identification of structures is on the right side of the figure. Scale represents 1 mm. For abbreviations see pages 166-167.

position of this structure as derived from the intrabullar cheirogaleid condition. As I suggest above, it is likely that a similar structural development occurred in the evolution of the tarsiiform morphotype from an adapid ancestry.

D represents a modified lemuriform condition, that of *Megaladapis*. Lamberton's (1941) studies on the bony ear region of the Madagascan primates revealed that the island species fall into two morphological groups as far as the position of the ectotympanic is concerned. He characterizes the first group (made up of *Archaeolemur*, *Hadropithecus*, *Mesopropithecus*, *Neopropithecus*, *Propithecus*, and *Lemur*), what is considered here the primitive lemuroid condition, as having either a very wide and short or nonexistent auditory canal (formed by the petrosal), an annulus tympanicus inside the bulla, free on part of its circumference, and a stapedial artery enclosed in a bony tube. Genera of his second group (*Megaladapis*, *Palaeopropithecus*, and *Archaeoindris*, i.e., the largest forms), have a bony and narrow external auditory canal, an annulus tympanicus attached entirely to the bulla, and a reduced (or possibly missing) stapedial branch not enclosed in a bony tube. Lamberton did not mention, however, that the external auditory tube is petrosal derived, although internally an extension of the annulus membrane is also ossified.

Dentition
Figures 147-155

It is difficult to assess what the most primitive omomyid, adapid, or paromomyiform molar morphology was. The inferred primitive condition of both omomyid and adapid molars was probably similarly primitive. Morphotypes of both of these groups, not very easily visualized, appear to be somewhat more advanced than an inferred primitive paromomyiform, and certainly more advanced in molar morphology than *Purgatorius*. In addition to these general remarks I cannot state with any degree of certainty whether the omomyid or adapid morphotypes were significantly different.

Whether the European tarsiiform genera (*Nannopithex*, *Necrolemur*, *Microchoerus*, and *Pseu-*

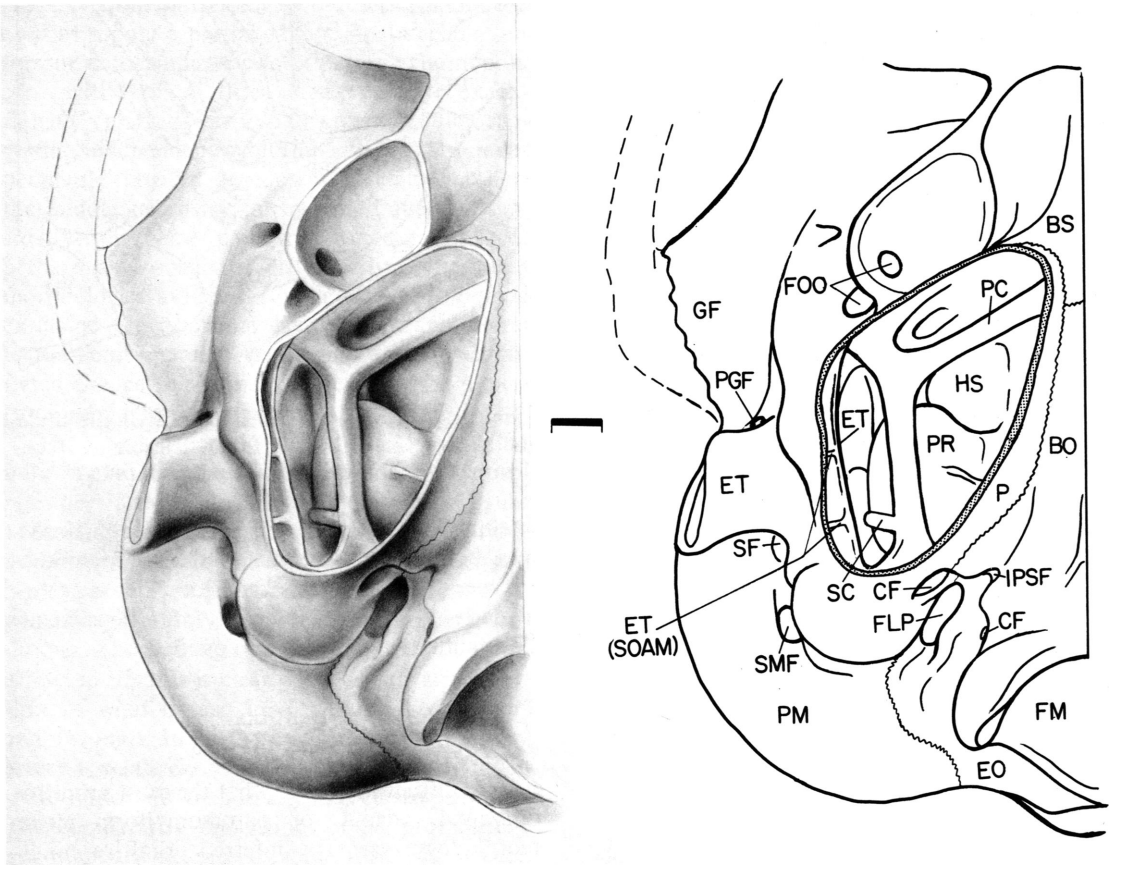


FIG. 144. Basicranial morphology of *Necrolemur antiquus* with only ventral floor of the bulla removed. Drawing is based on Montauban 9. Ventromedial view. Identification of structures is on the right side of the figure. Scale represents 1 mm. For abbreviations see pages 166-167.

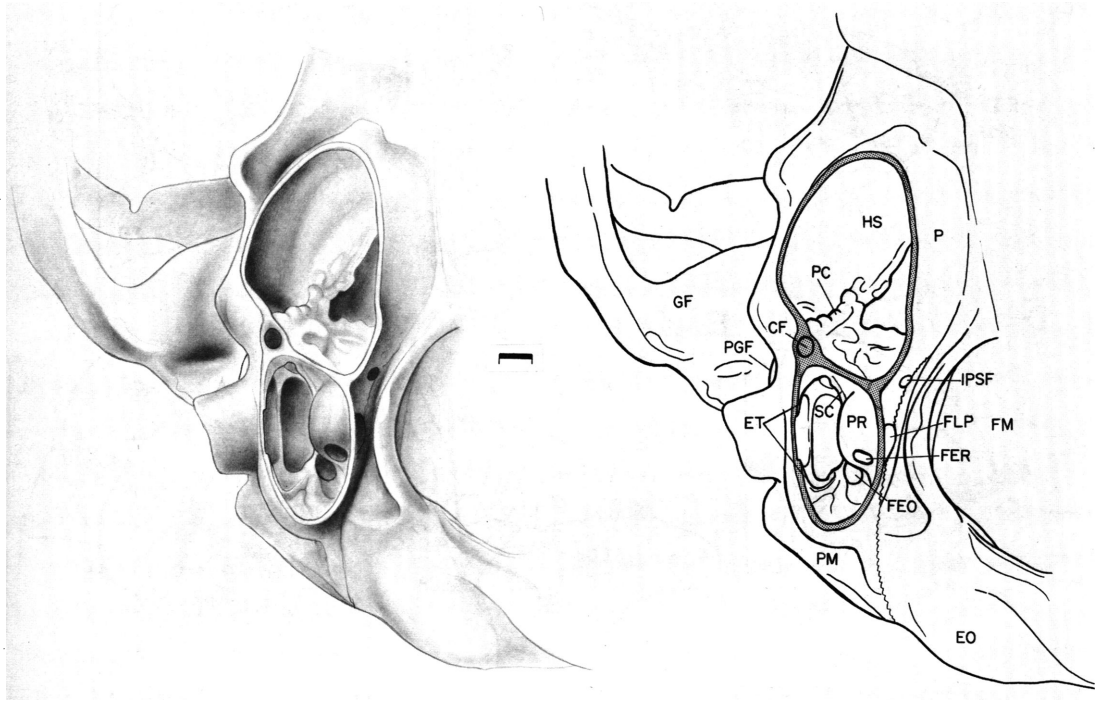


FIG. 145. Basicranial morphology of *Tarsius syrichta*, with only ventral floor of the bulla removed. Drawing is based on AMNH 150448. Ventromedial view. Identification of structures is on the right side of the figure. Scale represents 1 mm. For abbreviations see pages 166-167.

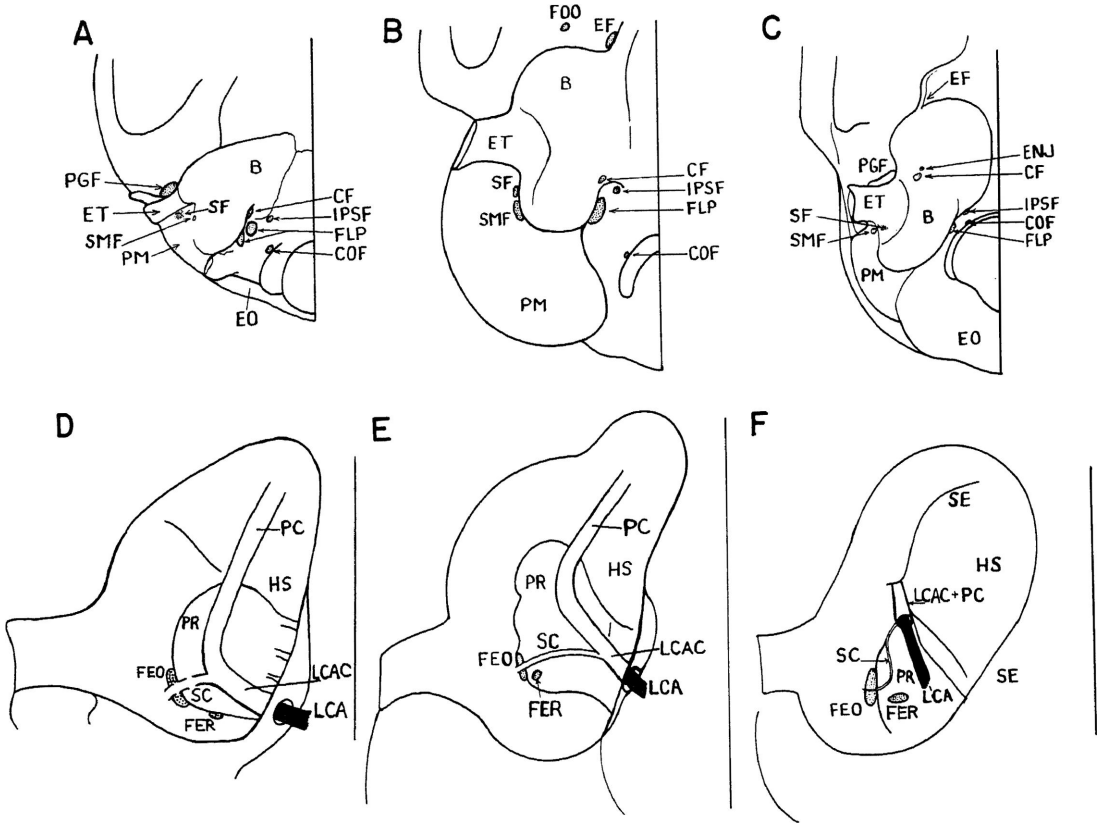


FIG. 146. Simplified schema of some aspects of basicranial morphology in a few known tarsiiform Haplorhini. A and D. *Rooneyia viejaensis* (earliest Oligocene); B and E. *Necrolemur antiquus* (medial or late Eocene); and C and F. *Tarsius* sp. (Recent). Above: basicrania intact, below: the bulla and ectotympanic are removed to show carotid circulation. Broken lines represent reconstruction. For abbreviations see pages 166-167.

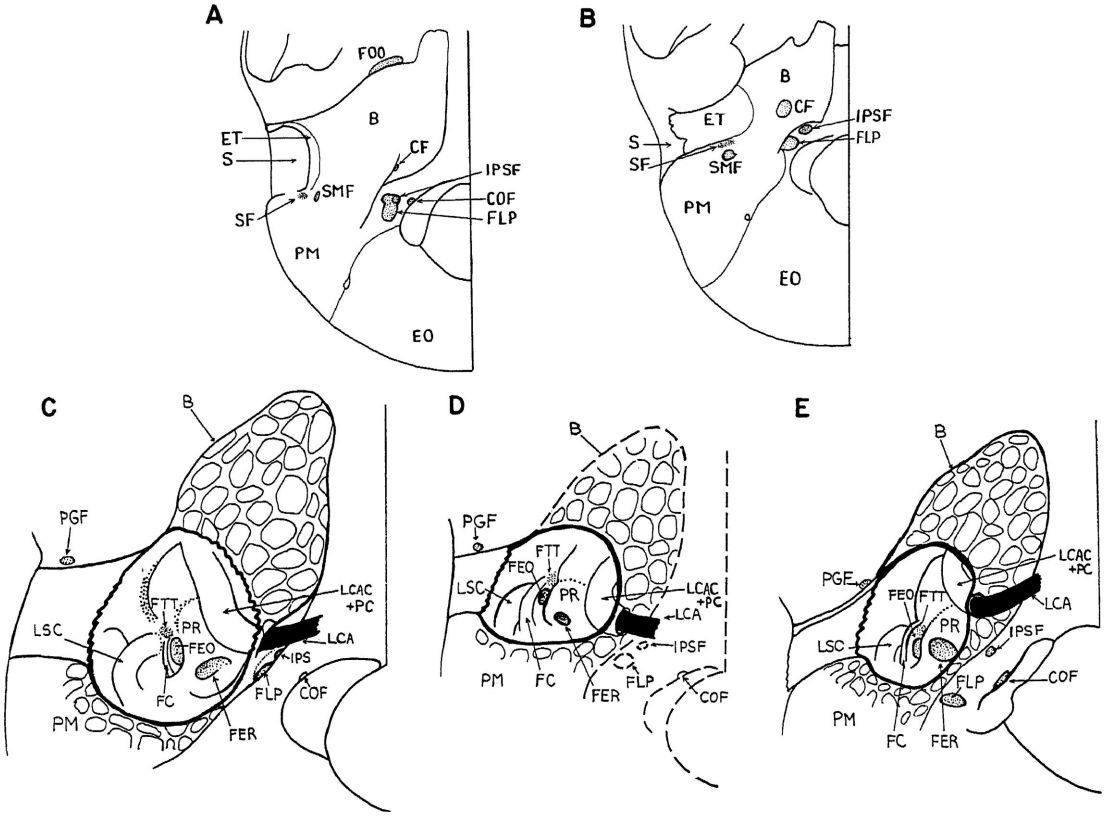


FIG. 147. Simplified schema of some aspects of basicranial morphology in a few representative genera of anthropoid Haplorhini. A and C. *Saimiri* sp. (Recent); B and E. *Cercopithecus* sp. (Recent); D. *Apidium* sp. (Oligocene, modified from Gingerich, 1973). Above: basicrania intact, below: the bulla and ectotympanic are removed and the internal architecture of the pneumatized regions is schematically shown. Heavy line around middle ear cavity shows where bone is cut to expose the morphology inside. Broken lines represent reconstruction. For abbreviations see pages 166-167.

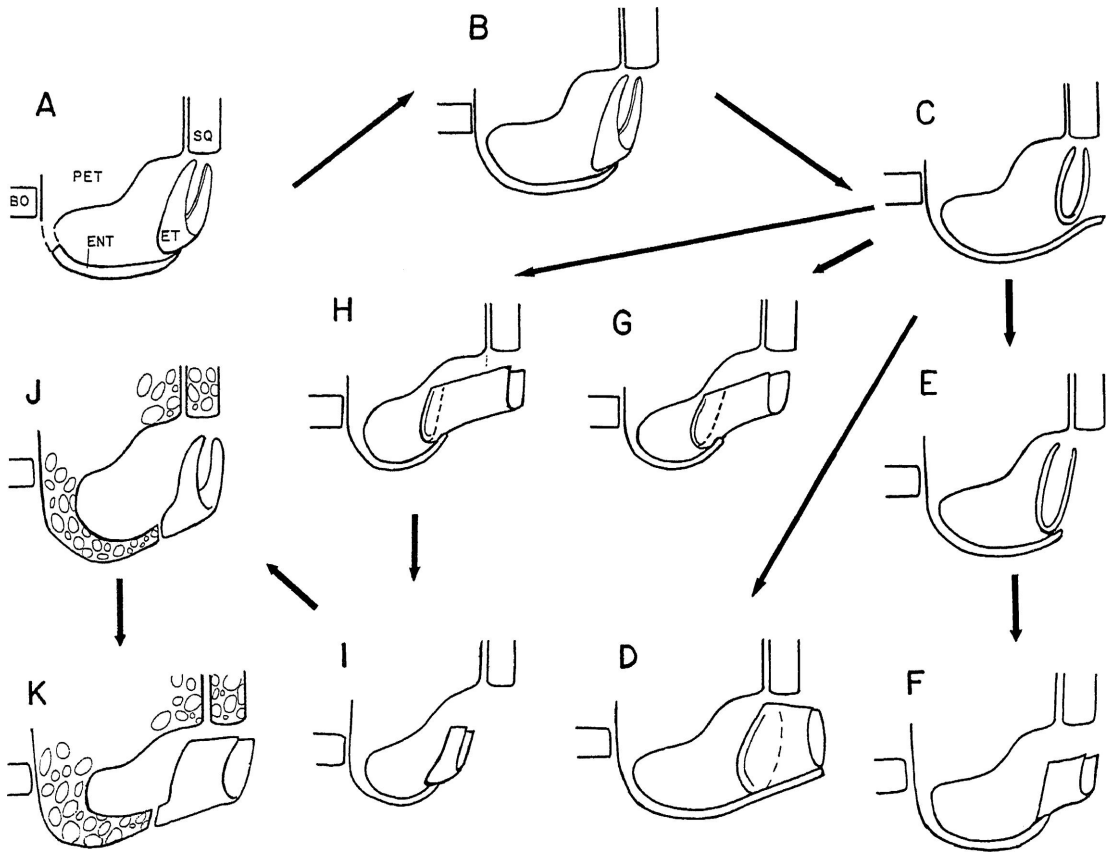


FIG. 148. Ectotympanic evolution in Primates. In this schema attempt is made to trace derivation of various ectotympanic conditions (other aspects of basicranium are ignored for clarity) from inferred antecedent states. Note that in this overview, primates have evolved bony "tube" at least three times independently from a condition that can be termed primitive lemuroid. As the mechanism for construction of this tube is extremely simple, involving only ossification of the annulus membrane, parallel evolutions are postulated for this derived condition in some paromomyiforms, tarsiiforms, and lorisiforms. External bony tube, in the catarrhines does not involve ossification of annulus membrane in same manner as in three previous groups.

A. Hypothetical ancestor. B. Intermediate between eutherian ancestor and primate morphotype. C. Primate morphotype, also probably primitive condition in the Strepsirhini. D. Modified lemuriform condition (e.g., *Megaladapis*) where petrosal elongated laterally and annulus membrane of ectotympanic also ossifies inside laterally expanded petrosal. E. Lorisid morphotype (e.g., *Galago*), slightly more advanced than that of cheirogaleids. F. Derived lorisiform condition (e.g., *Nycticebus*). G. Condition shown by *Plesiadapis*. Although morphology of ectotympanic is extremely similar to that of *Rooneyia*, other aspects of basicranium strongly suggest that ectotympanic conformations are convergent. H. Condition shown by *Rooneyia*, possibly representative of tarsiiform morphotype. I. Advanced (?) tarsiiform condition shown by *Necrolemur*. J. Platyrrhine morphotype. K. Condition known among living cercopithecoids and hominoids. Possibly representing catarrhine morphotype, although parallel evolution of this form of ectotympanic tube may have evolved independently from a catarrhine ancestor with condition similar to that shown on J. For abbreviations see pages 166-167.

doloris) are recognized as sufficiently divergent from the remaining early Tertiary tarsiiforms to represent an independent family or only a subfamily of the Omomyidae is a problem that should be dependent largely on the homologies of the antemolar dentition. If the homologies and the general conformation of these teeth can be shown to be the same as in most omomyid taxa then perhaps the derived nature of the basicranium of *Necrolemur* can be somewhat reconciled as acceptable and the Microchoerinae placed within the Omomyidae.

The most important first step in deciphering the homologies of the anterior teeth should be the establishment of the premaxillary-maxillary suture. Simons (1961b), who has attempted to solve the antemolar homologies of microchoerines and has extensively discussed some aspects of this problem, has bypassed the crucial issue by stating (p. 58): "the upper dental formulae of all species of both groups (i.e. of microchoerines and *Tarsius*) are apparently the same (2.1.3.3) as are the sizes of the teeth relative to each other . . ." This to me reflects the acceptance of the premaxillary-maxillary suture as originally shown for *Necrolemur antiquus* by Stehlin (1916, p. 1343) and by Simons and Russell (1960). Repeated examinations of all *Necrolemur antiquus* skulls in European and North American collections failed to confirm the suture mesial to the seventh tooth from the back or distal to the second one from the front. One specimen (MNHN 1957-14; fig. 149) may be interpreted as having had a suture pass between the first and second upper teeth. Fusion apparently at a very early stage in ontogeny occurred between the premaxillary and maxillary bones but this question is still unsettled. I know of no unequivocal evidence that would either support or contradict Stehlin's original designation.

Simons (1961b, pp. 58-61) argued that the enlarged microchoerine lower incisor is a canine. His evidence consisted of two specimens of *Microchoerus edwardsi* in the British Museum (Natural History) which, according to him, show small alveoli anterior to the enlarged procumbent tooth. He cited additional specimens of the same taxon in the Paris collections. My interpretation of these openings on specimens which are usually broken differs from his. I consider the openings as parts of the abundant nutrient canals on *Microchoerus* mandibles. This genus, for adaptive reasons obscure at present, had a great number of nutrient vessels entering and leaving the anterior part of the mandible. This condition is particularly well documented by the numerous, irregularly placed mental foramina on the side of the jaw (fig. 149). The discussion on occlusion by Simons (1961b, p. 57) is in general endorsed, but I believe that strict application of upper and lower tooth occlusal relationships cannot be applied to microchoerine dentitions. There are nine teeth above and seven below, although for all purposes of discussion the second lower tooth is so small that it takes no part in occlusion. Therefore, the number of operational lower teeth is better considered as six.

In order to analyze microchoerine tooth homologies and occlusion two important selective factors must be postulated. First, there was selection either for a reduced face, including both the upper and lower jaws, or selection operated to reduce the length of the lower jaw. Second, there was clearly selection for enlargement of the pair of anterior teeth both above and below. I will assume that phylogenetic enlargement of both upper and lower anteriormost teeth occurred simultaneously as their mechanical function and biological role are clearly closely tied together. The enlargement of the anterior teeth probably occurred together, and as the upper enlarged tooth is clearly not a canine, it is probable that the enlarged lower tooth is the incisor originally occluding with the enlarged upper incisor. This incisive function appears to have been of extreme importance judged by the selective size of the teeth in all microchoerines. Disturbance of the biological role of this important area therefore, by phyletically losing the lower incisor and replacing it with the lower canine seems unlikely. Selection for maintaining occlusion of a lower canine with an upper one was unlikely to be of greater importance than the maintenance of the adaptively important occlusion by the incisors. If this was the case then it is probably likely that following the enlargement of the anterior teeth, tooth reduction occurred distal to them. Clearly, not the same number of teeth were lost above as

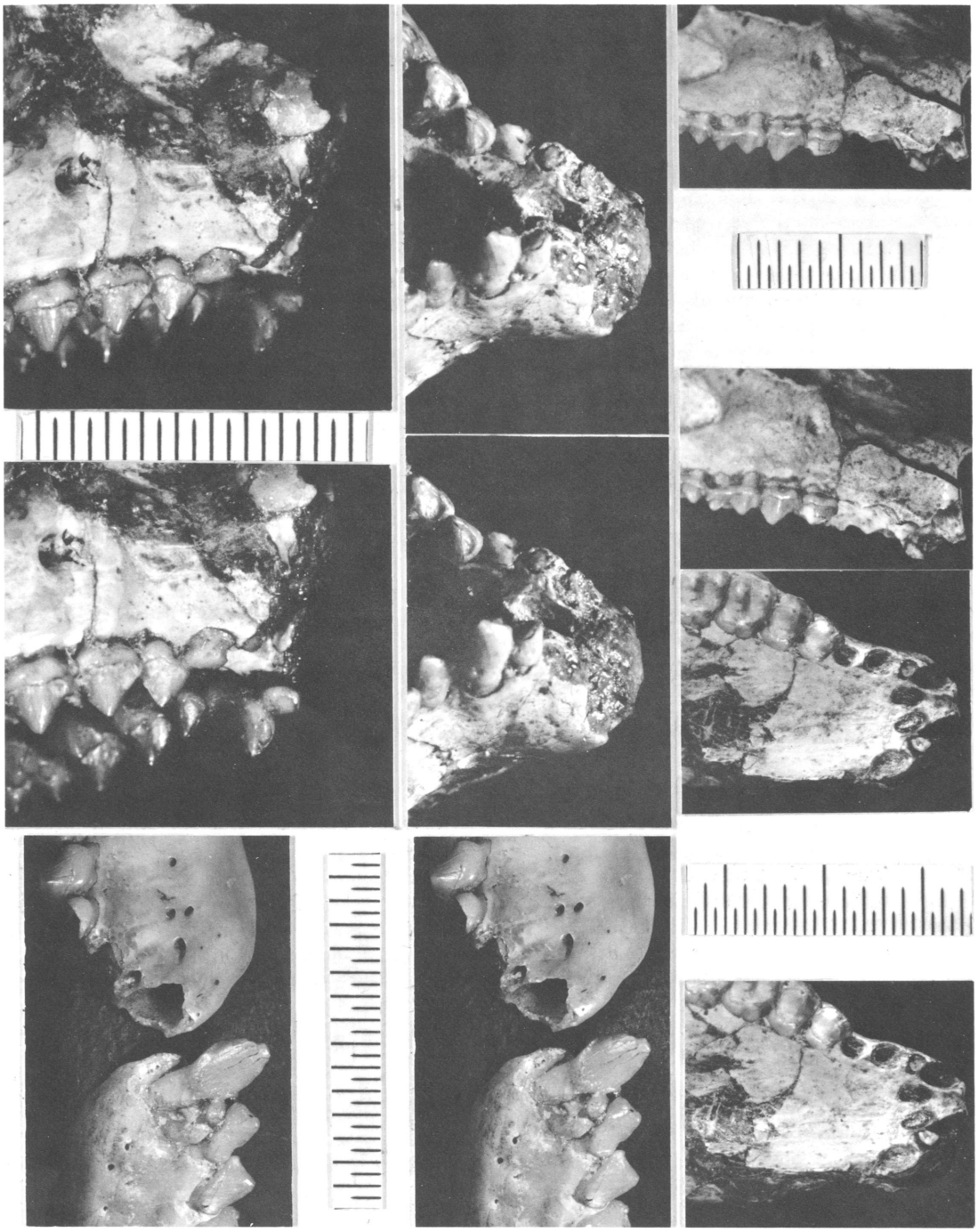


FIG. 149. *Necrolemur antiquus* specimens to show aspects of the anterior dentition for the determination of their homologies; MNHN 1957-14 (above left and center); Montauban 9 (right); and mandibles showing alveoli and nutrient foramina (below left); all from the Phosphorites of Quercy. Stereophotographs. Subdivisions on scales represent 0.5 mm.

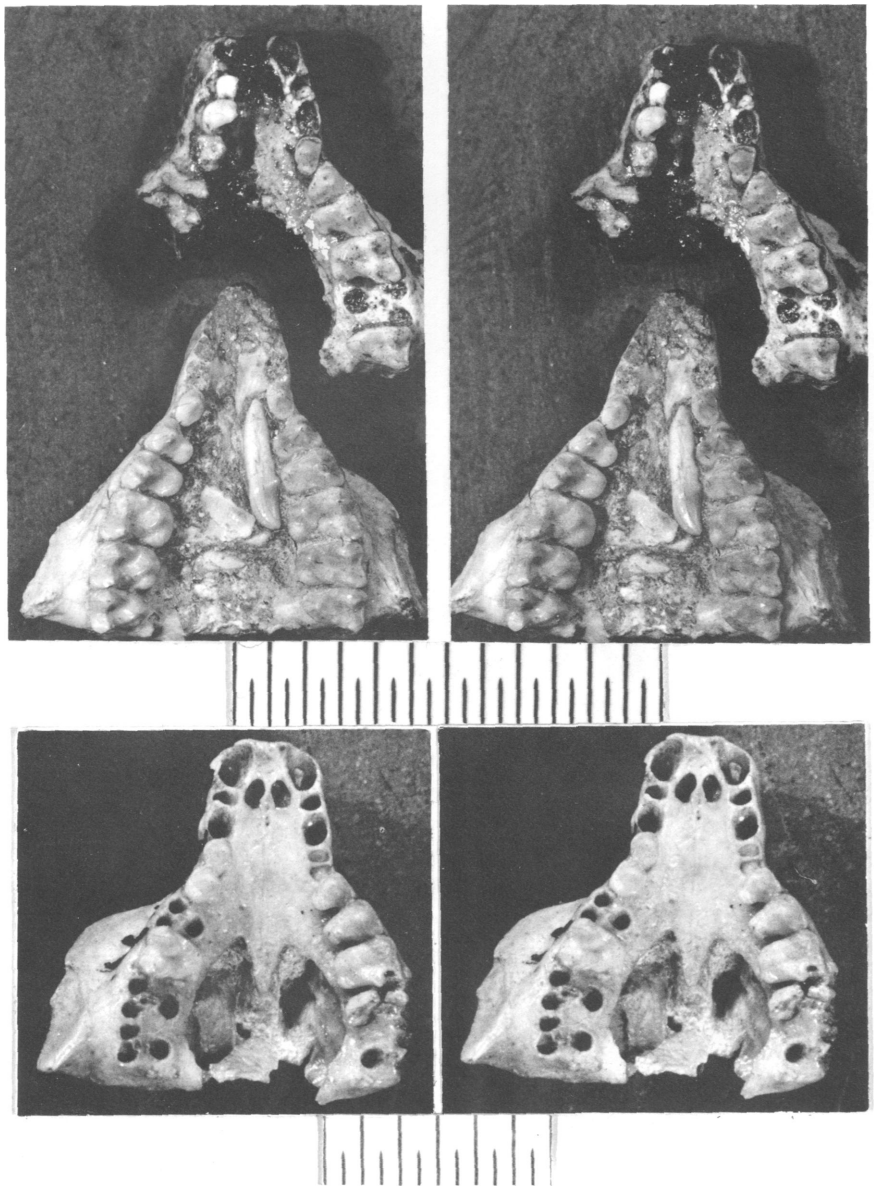


FIG. 150. *Pseudoloris parvulus*, two unnumbered palates (above) and MNHN V514 (below) from the Paris collections, all from the Phosphorites of Quercy. Stereophotographs: ventral (occlusal) views. Subdivisions on scales represent 0.5 mm.

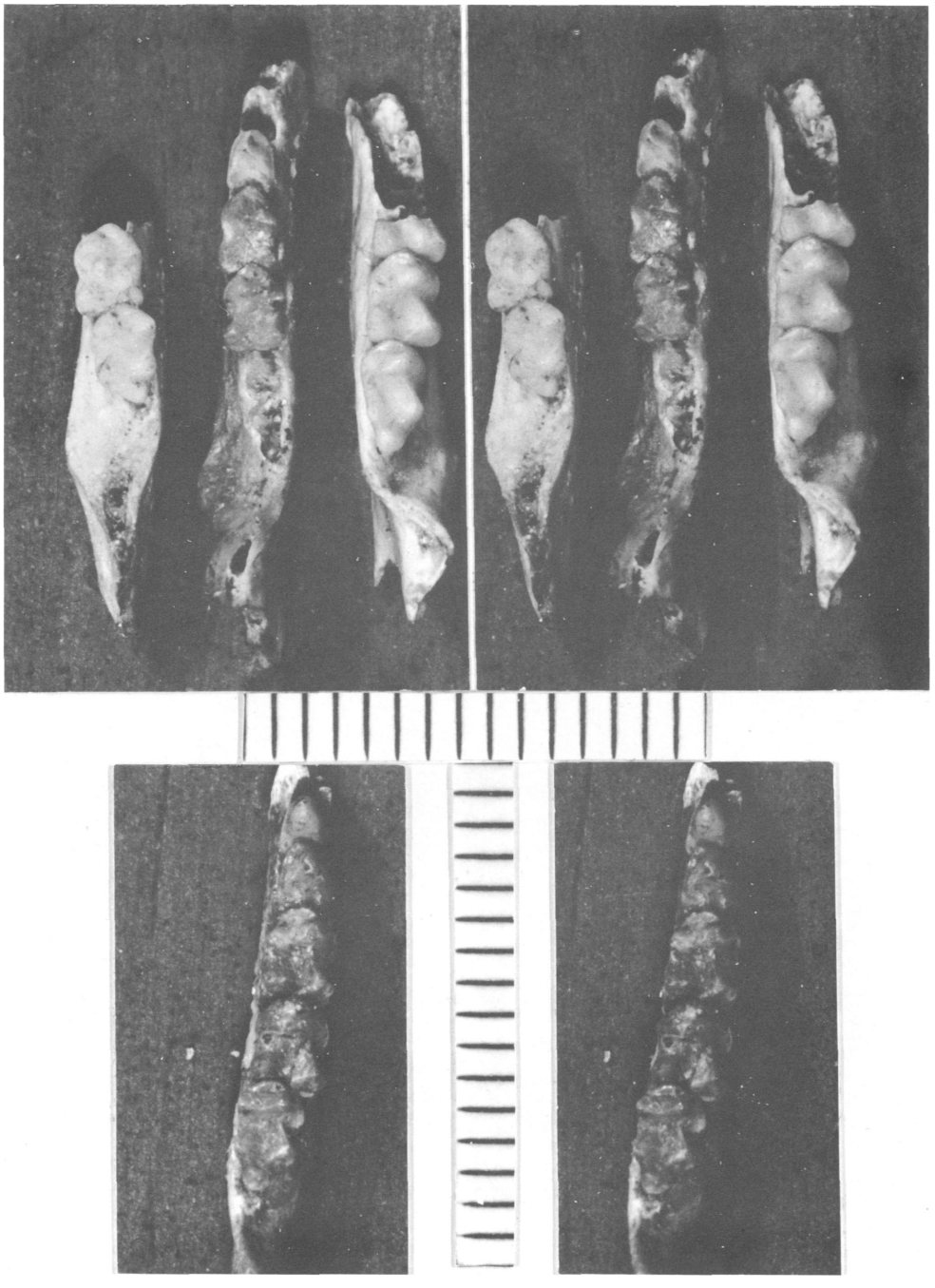


FIG. 151. *Pseudoloris parvulus*, unnumbered mandibles from the Paris collection, left M_{2-3} (above left); left P_4-M_2 (above center); right M_{2-3} (above right); and right P_3-M_3 (below); all from the Phosphorites of Quercy. Stereophotographs: occlusal views. Subdivisions on scales represent 0.5 mm.

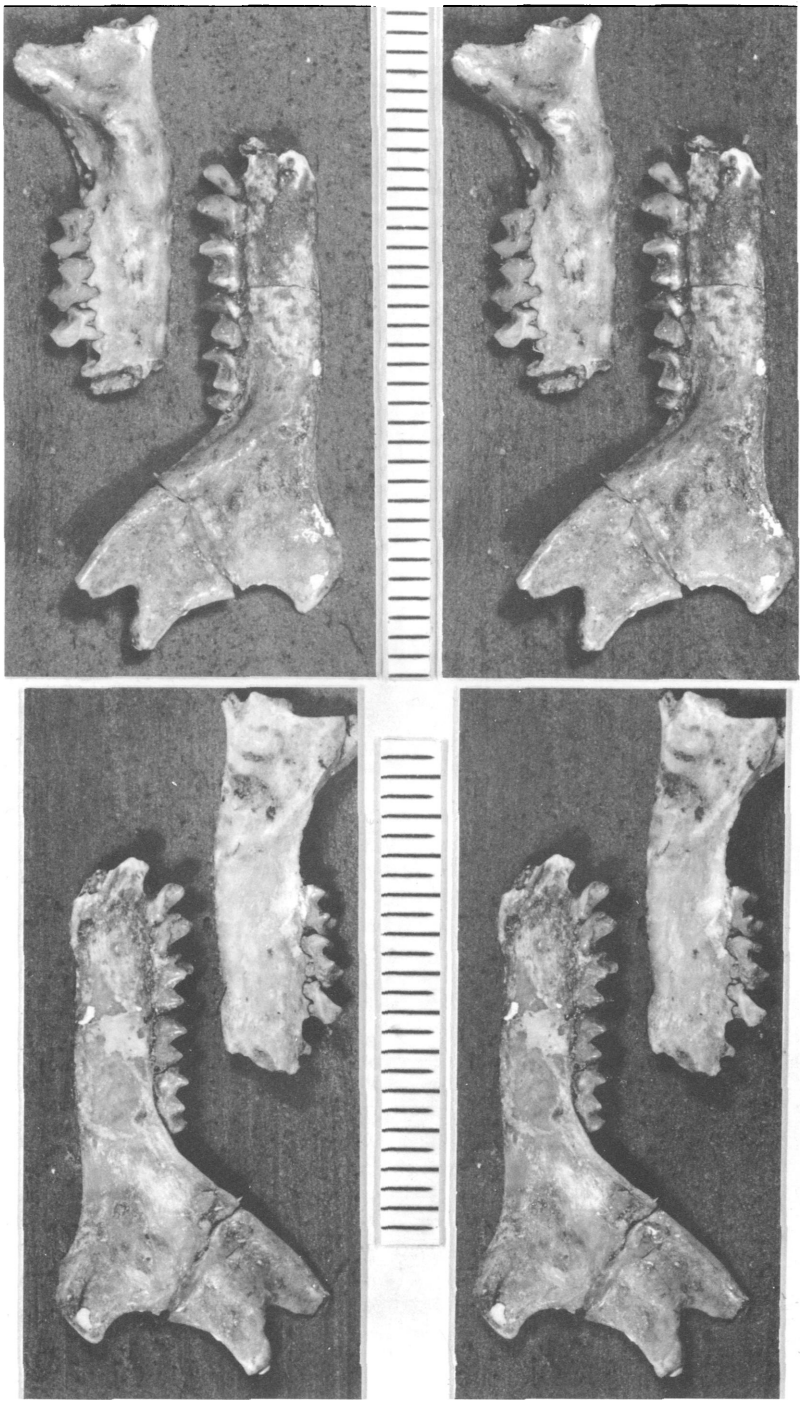


FIG. 152. *Pseudoloris parvulus*, unnumbered mandibles from the Paris collection, left P_4-M_2 (above left and below right); and right P_3-M_3 (above right and below left), all from Phosphorites of Quercy. Stereophotographs: lateral (above) and medial (below) views. Subdivisions on scales represent 0.5 mm.

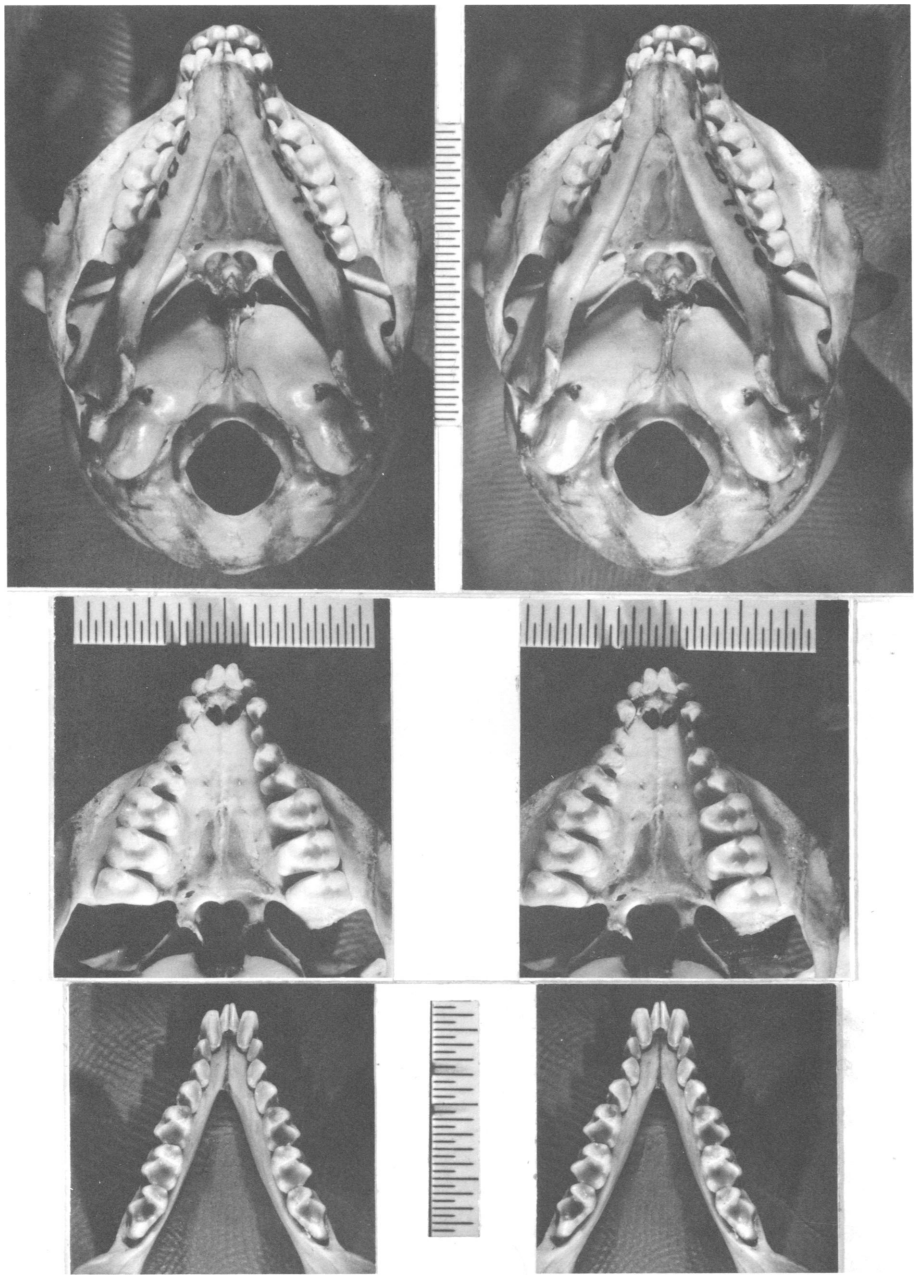


FIG. 153. *Tarsius* sp., male, AMNH(DM) 207006, Philippines, skull and mandible in ventral view in centric occlusion with mandible slightly anteriorly moved (above), upper dentition (middle), and lower dentition (below). Stereophotographs: ventral (above) and occlusal (middle and below) views. Subdivisions on scales represent 0.5 mm.

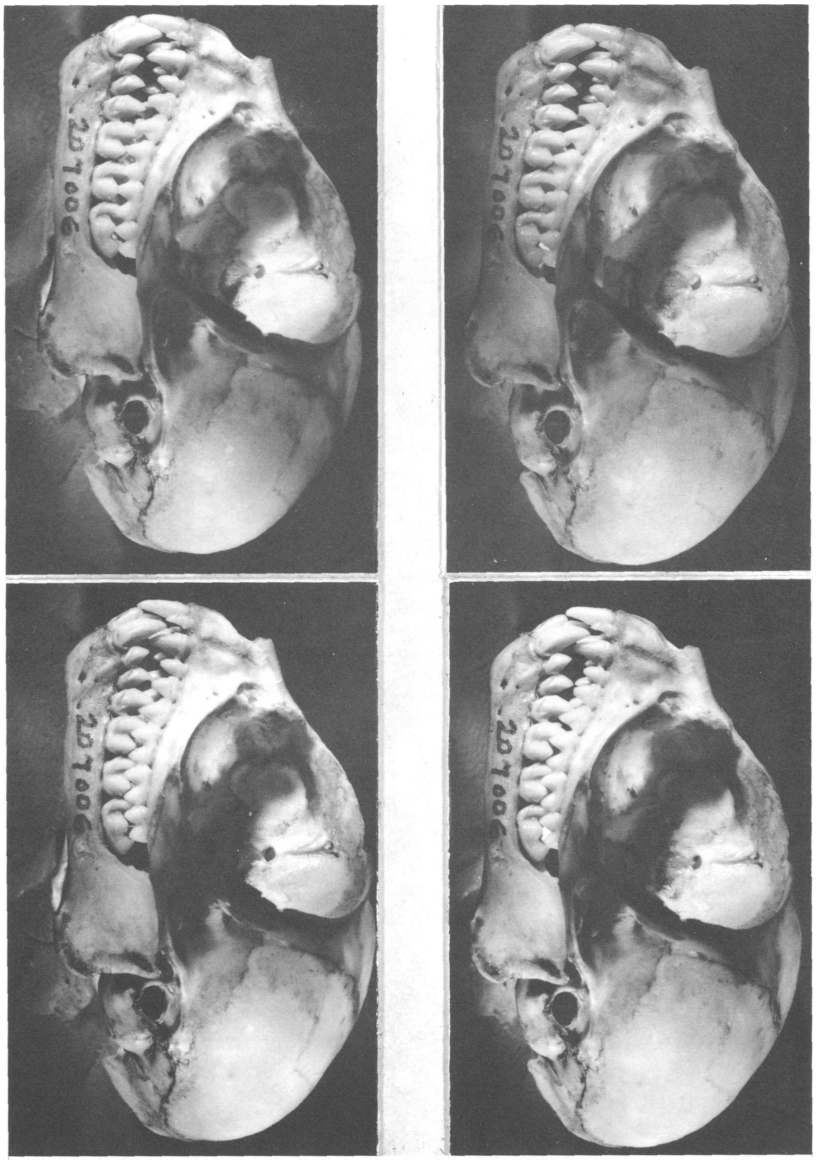


FIG. 154. *Tarsius* sp., male, AMNH(DM) 207006, Philippines, skull and mandible at onset of incisive stroke (above) and skull and mandible at onset of masticatory (= power) stroke. Stereophotographs: lateral views.

below. Thus as tooth reduction, a response to mandibular shortening, occurred it did so in a manner to fill the space on the mandible with the ontogenetically most developed teeth at the time of mandibular shortening.

Which of the upper teeth is most likely to be the canine? Lacking the evidence from the suture I cannot decide whether the second or third tooth from the front is the canine. In either case, in my view, the homology of the enlarged anterior teeth do not influence the decision about the upper canine.

The two teeth posterior to the enlarged lower incisor are either P_1 and P_2 as suggested by Simons or an incisor and a canine as I interpret the dental formulae in either *Omomys* or *Tetonius*, for example.

If the second upper tooth is the canine, then the derived enlargement of P^1 could be considered as a major distinction of microchoerines from all other tarsiiforms known. Therefore, their separation from the omomyids as a family, the Microchoeridae, could be supported.

Much has been made of the alleged similarities between the dentitions of the Quercy phosphorite *Pseudoloris* and that of *Tarsius* (see in particular Teilhard de Chardin 1916-1921, and Simons 1961b). Simons in 1972 emphasized again the resemblances between *Pseudoloris* and *Tarsius* and allocated the Microchoerinae to the Tarsiidae. Results of my re-examination of the similarities between *Pseudoloris* and *Tarsius* (figs. 150-152) differ from those of previous investigators. I found that some of the alleged similarities are not similarities at all, whereas others are convergent. The most important difference between the two genera, previously alleged to be similarities, is the manner of arrangement and occlusal function of the anterior dentition. These, in turn, strongly suggest, and this is borne out by the cheek tooth morphology, that the premolars and molars are similar due to convergence rather than as a result of deriving their conformation from a common ancestor.

The dentition of *Tarsius* and its inferred functional features are so unique that a brief account of the latter is necessary (for the morphology see figs. 153, 154). Articulating skulls with their mandibles suggest that a distinct incisive stroke is present. During this incisive bite the mesial edges of the lower canine shear against the greatly enlarged central upper incisors and the small lateral pair of incisors. The cutting edges of the two pairs of upper incisors are almost exactly transverse to the long axis of the skull. The molar crests are high and movement of the lower jaw appears to be mostly orthal with a very minimal mesiolingual component. The mandibular fossa is unusual among primates. Anteroposteriorly long and transversely narrow, it is a trough that permits extensive propalinal but very little transverse movement. The articular condyle also reflects this as it is long anteroposteriorly but very narrow transversely.

The arrangement of the anterior dentition of *Pseudoloris* is exactly like that of other microchoerines. Unlike the antecanine teeth of *Tarsius*, those of *Pseudoloris* are lined up mesiodistally. In addition to this pronounced difference the reduced microchoerine lower canine is not the major lower piercing tooth but this role is assumed by the enlarged incisor. The selection for the performance of the same biological roles, piercing and cutting, by the antecanine dentition, resulted in relative sizes, morphology, and the manner of mechanical function highly divergent and not similar between *Pseudoloris* and *Tarsius*.

Although the morphology of the postcanine teeth of *Pseudoloris* are similar to those of *Tarsius* there are several clues that the similarities are not shared derived character states. Close examination of the molars and the premolars reveals that the most important shared similarity between the two genera is the acuity of the cusps and the relatively high crests. Beyond these there are no similarities. *Pseudoloris* has a well-defined hypocone suggesting an ancestry not unlike *Nannopithex*.

Until we have proof as to the exact homologies of the upper teeth distal to the incisor, the Microchoerinae are best considered a subfamily of the Omomyidae, not of the Tarsiidae. As noted, microchoerines do not share some of the specializations of tarsiid ear regions. Short of a probably shared tarsiiform specialization of the tarsus and possibly the crus, they do not appear to share advanced traits exclusively with the Tarsiidae. Thus, in addition to the unique features of

the tarsiid feeding apparatus both its dental homologies and its unique function among the known tarsiiforms, the basicranial uniqueness of *Tarsius* (see above) would be sufficient to justify family rank separation of the Microchoerinae from the Tarsiidae.

There are very few specimens of omomyids known to me that show tooth replacement and consequently little can be said of individual species, let alone generalizations advanced for the family.

USNM 19198, a specimen of *Absarokius noctivagus* (fig. 50), described by Gazin (1958, p. 73), shows evidence for presence of replacement of the deciduous third and fourth premolars. The specimen shows that the permanent P_4 erupted after the first two molars and at about the same time or slightly after the third molar. The tooth Gazin suggests to be a P_2 is in my opinion a canine, a permanent one, erupting well after the first two molars have surfaced.

Another omomyid, which probably shows deciduous teeth, is AMNH 12598 (fig. 112), a specimen of *Uintanius ameghini*. The third and fourth premolars appear to be deciduous, and the molars were erupted while the deciduous premolars were still functioning.

A brief account on tooth replacement in *Tarsius syrichta* based on five specimens has been published by Dahlberg (1948). According to this author, only three of the permanent teeth replace deciduous ones, the canine and the third and fourth premolars. The following is the eruption sequence: $P\frac{2}{2}$, $dP\frac{3}{3}$, $dP\frac{4}{4}$, $I\frac{1}{1}$, I^2, $dC\frac{1}{1}$, $M\frac{1}{1}$, $M\frac{2}{2}$, $P\frac{4}{4}$, $C\frac{1}{1}$, $P\frac{3}{3}$, and $M\frac{3}{3}$ (see fig. 155B).

In contrast to tooth replacement in *Tarsius*, which is apparently very specialized, a study by Chase and Cooper (1969) on a slightly larger sample of *Saguinus nigricollis* shows a replacement pattern probably more nearly approaching a primitive haplorhine condition. They report the eruption sequence to be $dI\frac{1}{1}$, $dI\frac{2}{2}$, $dC\frac{1}{1}$ (the first three eruptions reported to be at birth, therefore the "sequence" given here is a "simultaneous" one), $dP\frac{2}{2}$, $dP\frac{3}{3}$, $dP\frac{4}{4}$, $M\frac{1}{1}$, $I\frac{1}{1}$, $I\frac{2}{2}$, $M\frac{2}{2}$, $P\frac{4}{4}$, $P\frac{2}{2}$, $P\frac{3}{3}$, and $C\frac{1}{1}$ (see fig. 155A). For comparison, an eruption sequence for gibbons (Schultz, 1973) and

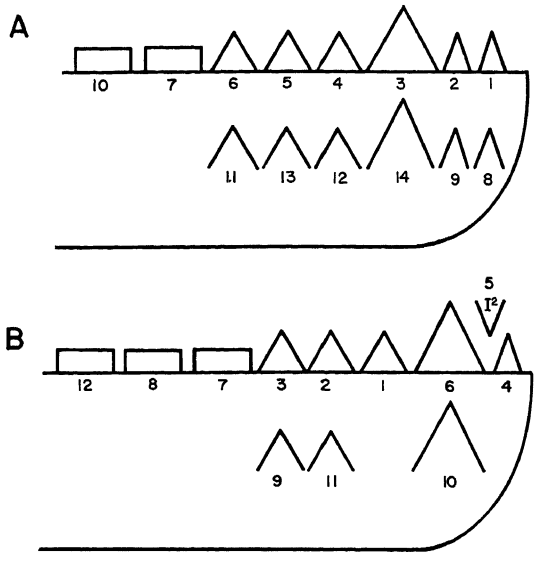


FIG. 155. Tooth eruption sequences in the lower jaw of *Saguinus nigricollis*, A (based on data from Chase and Cooper, 1969); and *Tarsius philipensis*, B (based on data from Dahlberg, 1948).

for that matter most living cercopithecids and man is as follows: $dI\frac{1}{1}$, $dI\frac{2}{2}$, $dP\frac{3}{3}$, $dC\frac{1}{1}$, $dP\frac{4}{4}$, $M\frac{1}{1}$, $I\frac{1}{1}$, $I\frac{2}{2}$, $M\frac{2}{2}$, $P\frac{3}{3}$, $P\frac{4}{4}$, $C\frac{1}{1}$, $M\frac{3}{3}$. As Schultz (1973, p. 14) noted, "in all three great apes the second molars normally erupt before the canines which are their last deciduous teeth to appear."

Admittedly, there is very little fossil tarsiiform evidence for replacement. Yet it appears reasonable to assume that replacement of only three teeth by *Tarsius* is not representative of the primitive omomyid condition and the callithricid *Saguinus* is probably more similar in this respect to the tarsiiform ancestry than are the tarsiers.

Postcranial Morphology
Figures 156-173

As for the cranium, the available specimens permit only somewhat haphazard glances at the postcranial skeletal morphology of the family. No single species is known by a complete skeleton, and the vertebral column and the hand are entirely unknown for any member of the family.

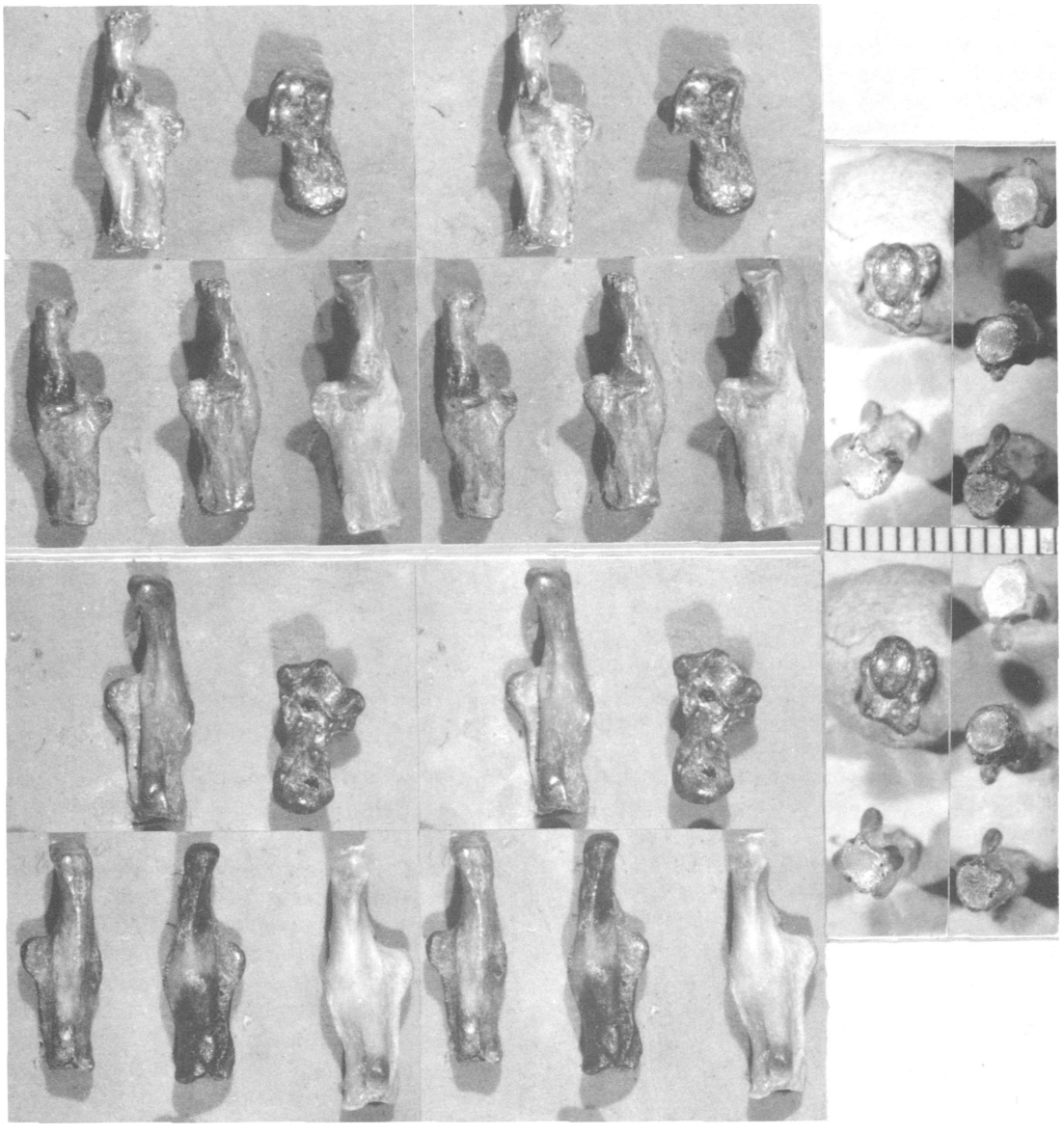


FIG. 156. *Teilhardina belgica*, calcanea and an astragalus from Dormaal, Belgium. Stereophotographs: dorsal (above), ventral (below left), and distal (left right) views. Subdivisions on scale represent 0.5 mm.

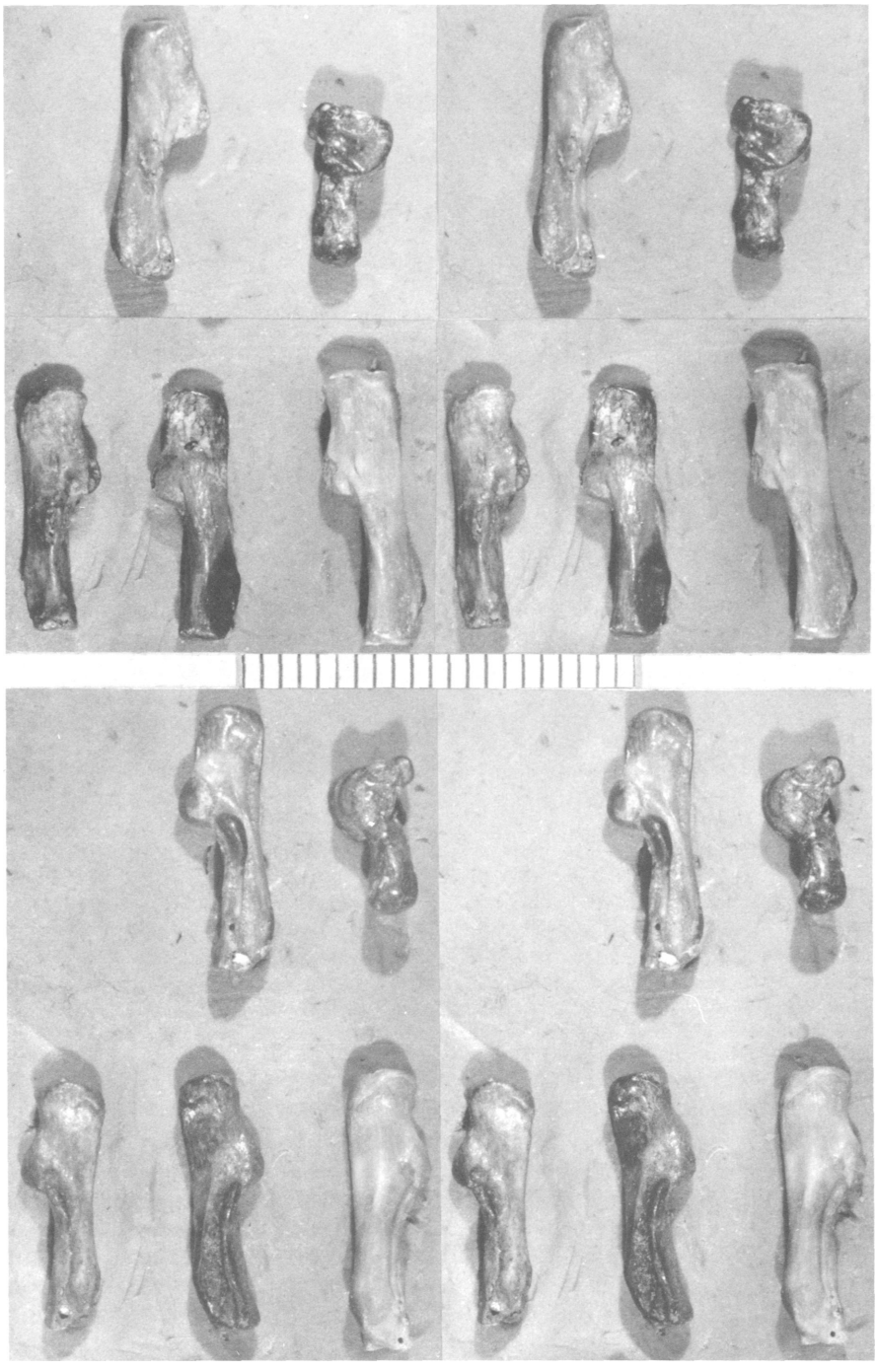


FIG. 157. *Teilhardina belgica*, calcanea and an astragalus from Dormaal, Belgium. Stereophotographs: lateral (above) and medial (below) views. Subdivisions on scale represent 0.5 mm.

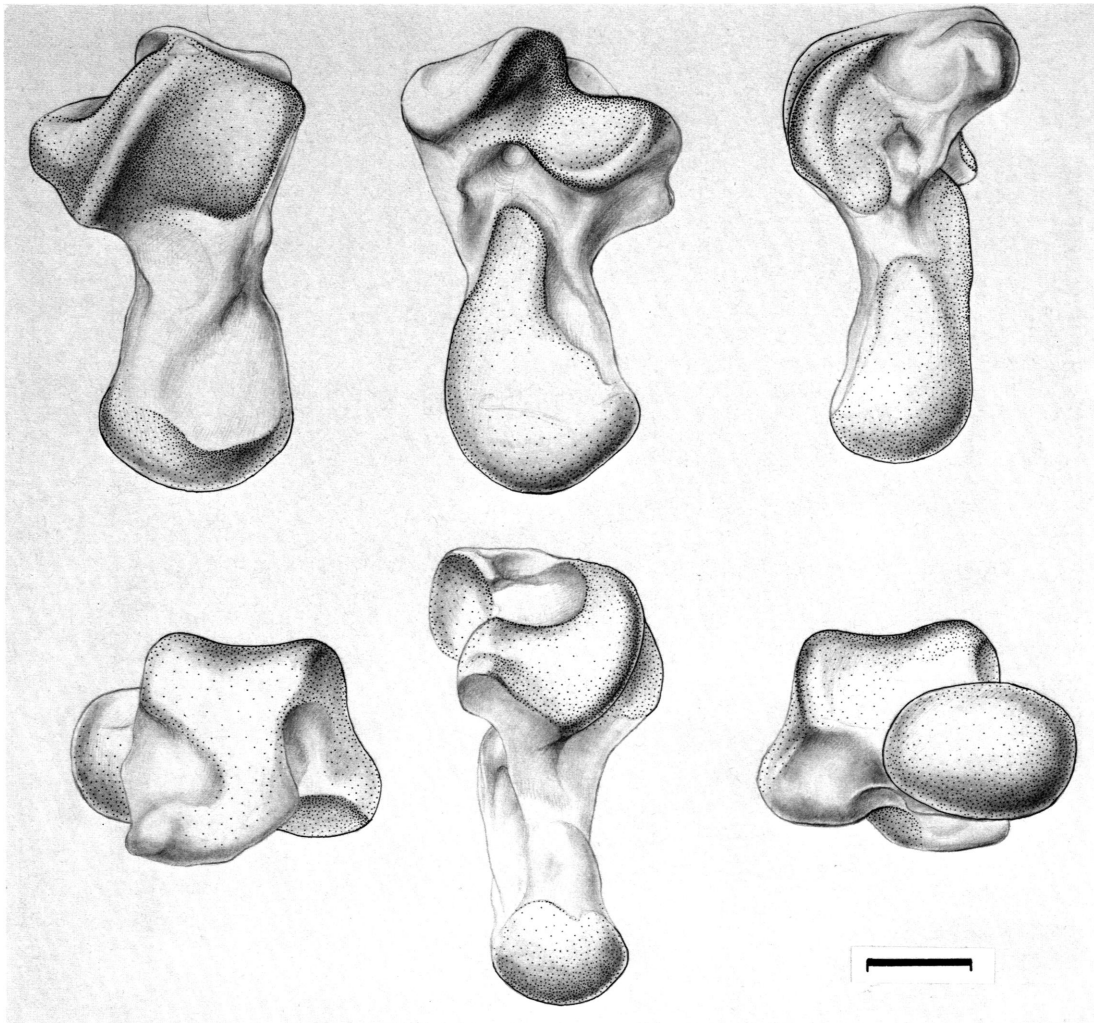


FIG. 158. *Teilhardina belgica*, right astragalus, based on IRNSB 4386, Sparnacian, Belgium; from left to right above: dorsal, ventral and medial view; from left to right below proximal, lateral, and distal views. Stippled areas represent probable joint surfaces. Scale represents 1 mm.

The most complete skeletal remains of any omomyid is still the fragmentary skeleton of *Hemiacodon gracilis*, AMNH 12613. Simpson (1940, p. 190-197) described this skeleton, and as I do not present a functional analysis of the postcranial anatomy in this study, the specimens will not be redescribed in detail. New illustrations of these are presented, however.

Simpson (1940, pp. 195-197) rightly emphasized that the skeletal remains of *Hemiacodon* were close to his morphological concept of the Lemuroidea. The latter, judged from his comparisons, included as phenetically, temporally, and phyletically widely separated forms as *Notharctus*, *Lemur*, and *Galago*. In particular the last genus was to typify the long-footed lemuroids for Simpson. Simpson referred to lemuroid characters throughout the discussion but it is difficult to ascertain which particular species he had in mind. He concluded that *Hemiacodon* was skele-

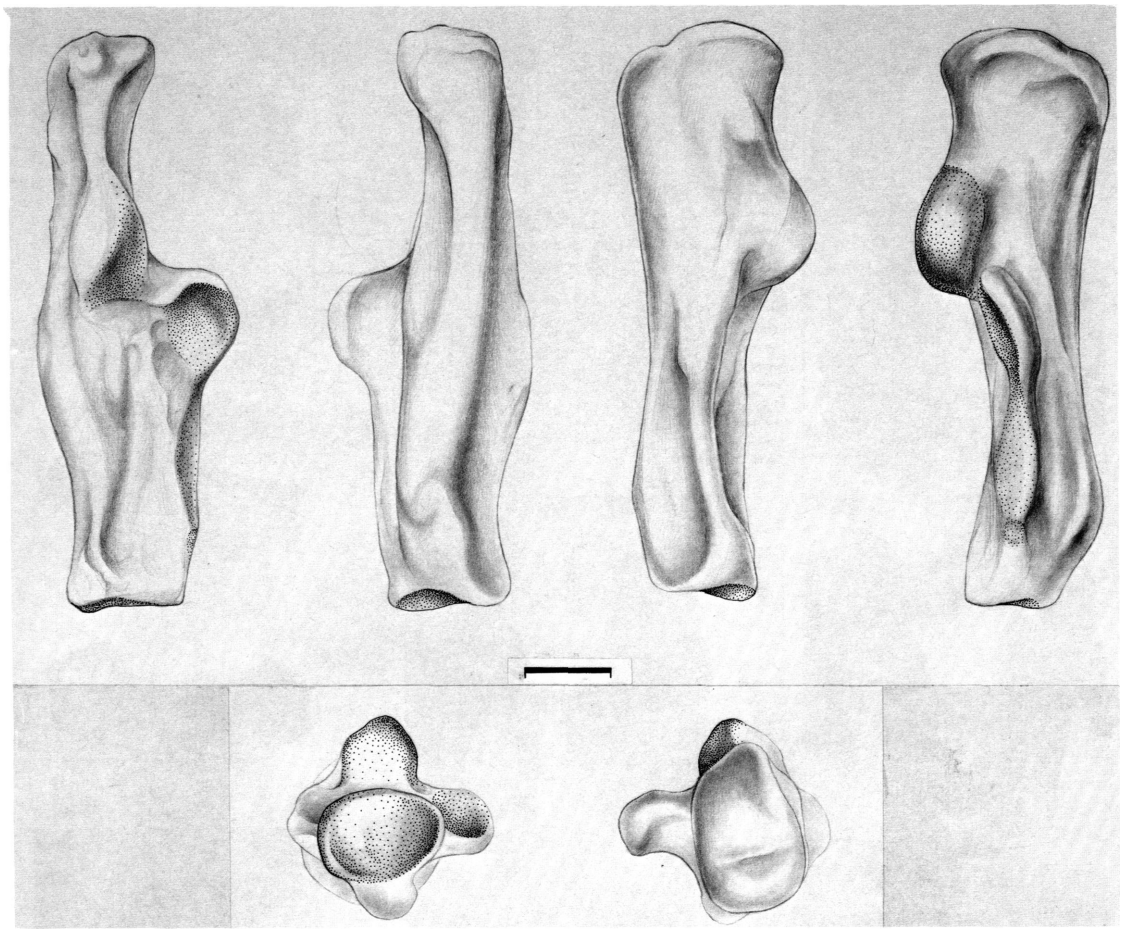


FIG. 159. *Teilhardina belgica*, right calcaneum, based on IRNSB 61, 4385, and 4390, Sparnacian, Belgium; from left to right above: dorsal, ventral, lateral, and medial views; from left to right below distal and proximal views. Stippled areas represent probable joint surfaces. Scale represents 1 mm.

tally "intermediate" between tarsioids and lemuroids. He also suggested the possibility (p. 197), improbable to him, "either (1) that *Hemiacodon* and its allies are true and fully differentiated tarsioids resembling the lemuroids only by convergence or in pre- or proto-primate characters, or (2) that they are lemuroids convergent toward the tarsioids in some respects."

Perusal of Simpson's discussion of the postcranial anatomy of *Hemiacodon* indicates to me that at that time his overriding concern was the discovery of general similarity which would align the genus with either *Tarsius* or the "lemuroids" (i.e., the category Strepsirhini). His aim was phenetic resemblance in the morphology rather than recency of ancestry. He could not find diagnostic features, and in this respect the "intermediate" phenetic position of *Hemiacodon* between *Galago* and *Tarsius* is largely correctly ascertained. The concept "lemuroid" was used, however, in a rather objectionable sense in the study. I believe that comparisons of the bones, such as the calcaneum, with various characters of *Galago* rather than with those of an inferred ancestral condition of the "lemuroids" (i.e., strepsirhines) biased his discussion. Thus, comparisons with

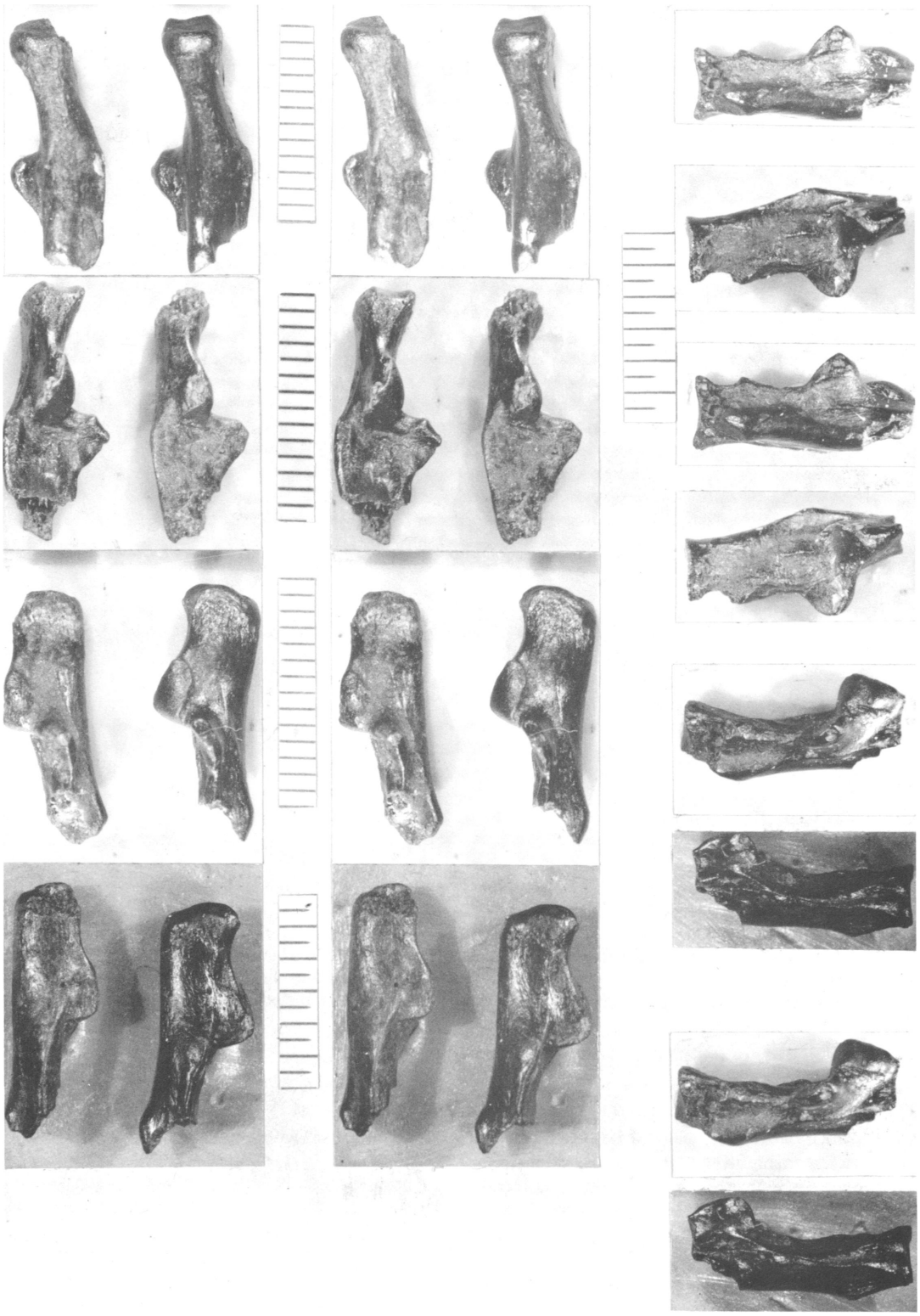


FIG. 160. Anaptomorphine, probably *Tetonius homunculus*, AMNH 88821, right calcaneal fragment (left); AMNH 88823, right calcaneal fragment (center); and AMNH 88820, right calcaneal fragment (right); all from East Alheit Pocket, Wasatch beds. Stereophotographs: plantar (above), dorsal (top middle), medial (bottom middle), and lateral (below) views. Subdivisions on scales represent 0.5 mm.

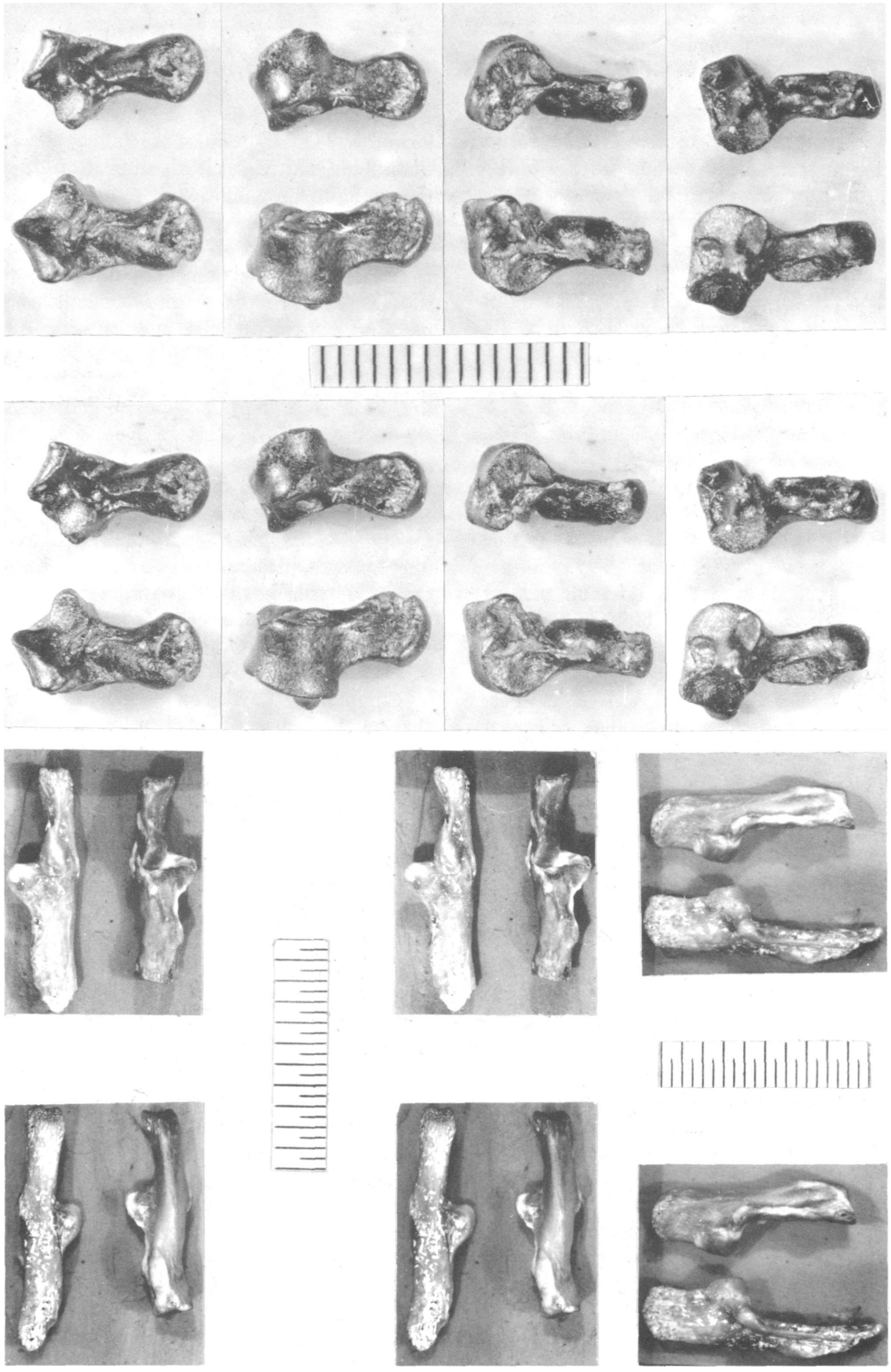


FIG. 161. Anaptomorphine, probably *Tetonius homunculus*, AMNH 88818, left astragalus (above top); AMNH 88817, right astragalus (above bottom); both from East Alheit Pocket, Wasatch beds. Omomyine A, AMNH 88886, loc. 5, Hyopsodus Hill, Bridger beds, left calcaneum (below left and below right bottom). Omomyine B, AMNH 88824, Lost Mountain, loc. 3, Bridger beds, right calcaneum (below center and below right top). Stereophotographs: plantar (above extreme left and middle left), dorsal (above left and below left), medial (above center right and below right), and lateral (above right) views, respectively. Subdivisions on scales represent 0.5 mm.

Adapis, *Notharctus*, and other Eocene forms were rewarding, not only because of the antiquity of the European taxa but because of the clearly primitive strepsirhine characters of such known elements as the astragalus and calcaneum (Decker and Szalay, 1973).

Simpson (1940, p. 195) correctly pointed out that calcanea of *Hemiacodon* and *Teilhardina* are similar and, although stated differently, he concluded that the similarities indicated close relationships. While in Halle, DDR, in 1970 I attempted to locate the calcaneum and tibia-fibula described and poorly illustrated by Weigelt (1933). Search by Professor Matthes failed to locate these specimens. As Simpson (1940, p. 196) pointed out, the poor illustrations of the postcranials mistakenly allocated to *Pseudoloris* by Weigelt (1933) show "considerable resemblance to *Hemiacodon* in the hindlimb." I might further add that, in light of the complex of similarities which tie microchoerines to omomyids and which I judge to be derived features, there is no reason to suspect that calcaneal elongation of *Nannopithex* and *Necrolemur* is not an equally shared character inherited from a common omomyid ancestry.

Broadly based studies on the evolutionary morphology of early Tertiary primate skeletal remains are under way and the results will be published at later dates. Some pertinent analyses have already been communicated (Szalay and Decker, 1973; Decker and Szalay, 1973) on the then known foot structure of paromomyiforms and Eocene lemuroids. At this time, however, selected parts of the postcranial anatomy offer some additional information for the assessment of omomyid phylogeny. Because tarsal remains, the calcaneum and astragalus in particular, are known from more early Tertiary species of primates than any other parts of the postcranial anatomy, these elements are excellently suited for broad comparative studies among a whole range of species and supra-specific categories. Occasional long bone fragments or pelvic remains are not so well known, therefore, at present, their value for phylogenetic and functional analyses is considerably less.

Several different kinds (at least on the species but more likely on the generic level) of calcanea and astragali are known from various Eocene localities. These tarsals are almost certainly omomyids, although clearly allocation to genera is uncertain. Probabilities of referral to dentally described taxa vary from locality to locality. Thus, calcanea and an astragalus (figs. 156-159) from Dormaal, Belgium, are almost certainly those of *Teilhardina belgica*. Nonadapid and nonparomomyiform calcanea and astragali from the Four-Mile localities of Colorado (figs. 160-162) are likely to be remains of one of the two species of *Tetonius* present. The possibility exists that the tarsals are those of *Mckennamorphus* but this is less likely on grounds of relative abundance. The dental remains of the probably nonprimate microsyopid *Niptomomys* are very small in dimensions in comparison with the tarsals to have a likelihood of both belonging to the same animals. Omomyid calcanea, which are not *Hemiacodon*, are known from Bridger beds (see omomyine A on fig. 161 and omomyine B on figs. 161 and 163).

Comparisons have been made with virtually all the known relevant fossil primate record and with representatives of all genera of extant primates. Among the living taxa particular emphasis was placed on strepsirhines, *Tarsius*, and platyrrhines. The most significant of the comparisons, as the discussion below hopes to reveal, have been those with the Paleocene and Eocene fossil record. Without attempting to be exhaustive, I will briefly examine several selected features of the omomyid tarsals. The following characters will be considered: 1) relative lengths of moment arms of the calcanea, 2) the calcaneocuboid articulation, 3) the peroneal tubercle, 4) the lower ankle joint between the astragalus and calcaneum, 5) the astragalonavicular articulation, and 6) the tibial trochlea, the astragalar canal, and the upper ankle joint, in general.

Calcaneal elongation appears to characterize as phyletically distant genera of omomyids as *Hemiacodon*, *Teilhardina*, *?Tetonius*, the Bridger omomyids (with generically uncertain allocation), *Necrolemur*, and *Nannopithex*. Until proved to the contrary, it appears reasonable to assume that calcaneal elongation shown by these taxa is an ancestral omomyid character. This character, if validly inferred to be primitive for the omomyids, separates the family from any known paromomyiforms or the primitive condition in-

ferred for adapids. The traditional explanation of lever arm shortening and "load" arm elongation of the calcaneum centered on the alleged increase in the speed of plantarflexion of the foot during the push-off phase of the jump and the increased mechanical advantage for jumping longer distances. The mechanics of this problem have not been satisfactorily evaluated, so comments on the adaptive value of this complex are difficult to appraise. One may suggest for the time being that these features of omomyid calcanea possibly indicate a greater propensity for habitual jumping than those of other known early Tertiary primates.

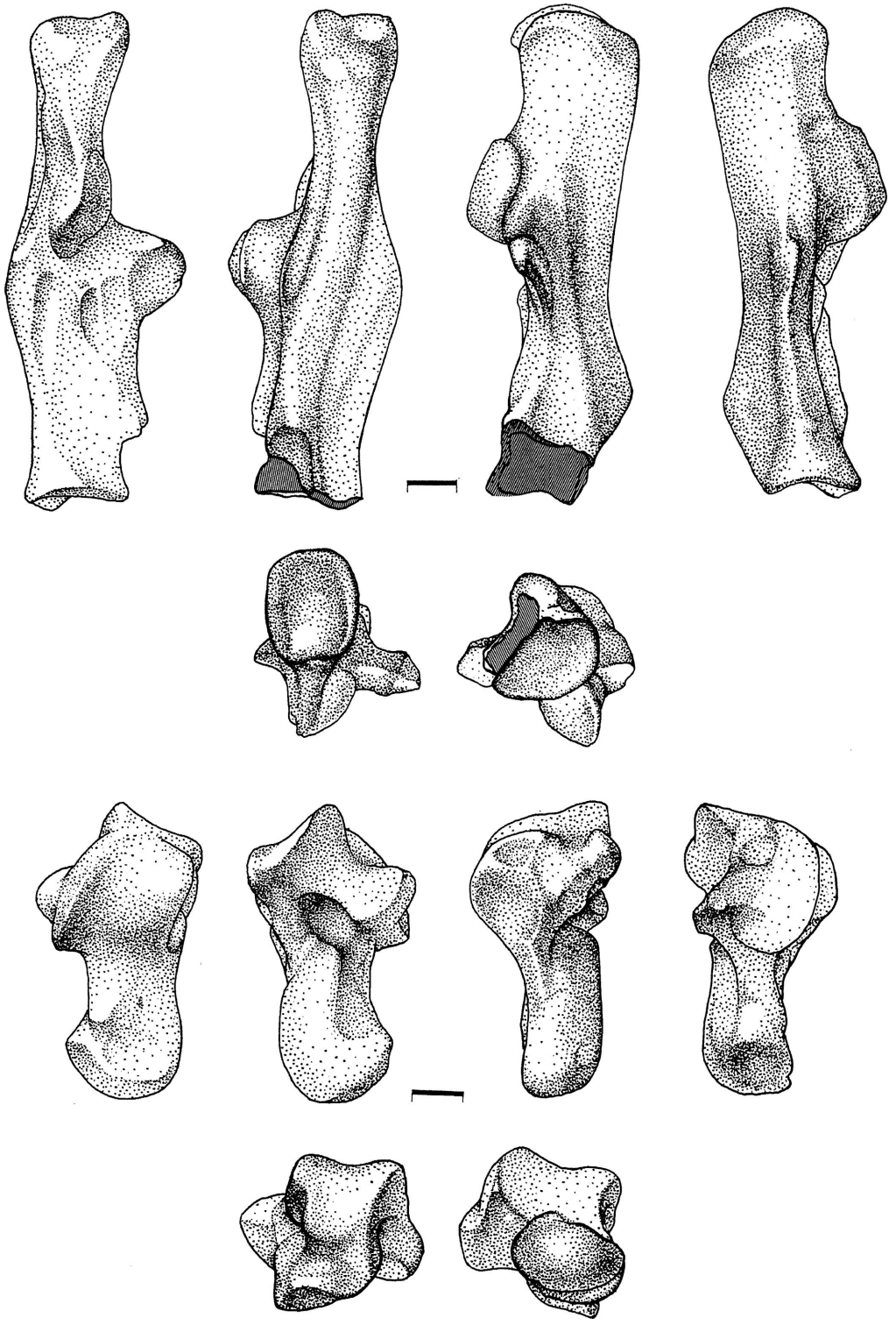
Comparisons of omomyid tarsals with those of adapids reveal that relative elongation of the moment arm is advanced in *Hemiacodon* and others as it is in *Microcebus* or *Galago*. Combined characters of any of these taxa, therefore, when compared with one another, indicate that this feature was independently attained in cheirogaleids and lorisids on the one hand and the omomyids on the other.

The importance of the calcaneocuboid articulation for mammalian feet has been discussed in detail by Szalay and Decker (1973). Selection for the characteristic calcaneocuboid joint among primates (and arboreal metatherians also) was to facilitate mediolateral rotation of the pes anterior to the calcaneum. This was brought into operation to accomplish extremes of inversion and, in general, mobility of the pes to grasp the substrate along a spectrum of positions. Such selection pressures are likely to have been produced in an arboreal substrate. Evolution of a calcaneocuboid pivot, then, is an essential part of a mobile and stable character complex to accomplish the needs of most advanced arboreal mammals. Yet, in *Tarsius* cuboidocalcaneal facets do not show the well-developed socket for the pivot as do, for example, *Hemiacodon*, *Teilhardina*, ?*Tetonius*, or the Eocene lemuroids (see Decker and Szalay, 1973).

Is the lack of a well-developed cuboid pivot in *Tarsius* primitive or derived? At first it would appear that the plantarly shallow cuboidocalcaneal facet represents a structural stage possibly intermediate between those of paromomyiforms and adapids. The lack of a peroneal process, the elongated moment arm, and a transversely oriented cuboidocalcaneal facet, however, suggest otherwise. These characters appear to be changes correlated with the development of a primate calcaneocuboid system selected for the biological role noted below.[1]

There is no peroneal tubercle, as such, known among omomyid calcanea. Eocene adapid remains do show slight remnants of this primitive eutherian structure associated with the peroneus muscles. As pointed out by Decker and Szalay (1973) considerable problems exist in the determination of the homologies of this structure in lemuriforms as the calcaneofibular and astragalocalcaneal ligaments sometimes attach in the same area, causing the development of nonhomologous tuberosities. In spite of the difficulties it can be determined that the adapid condition of the pe-

[1] Unlike known omomyids, the extant *Tarsius* lacks a cuboid pivot. I suspect that its absence is a derived condition from an ancestor which possessed it. Why would a group of primates with morphological characters from any of the known articular areas of the postcranial anatomy showing entrenched adaptations for an arboreal mode of life diminish an attribute such as the calcaneocuboid pivot? There are two functional reasons which may cause the reduction of the pivot. When leaping, *Tarsius* fulcrumates on a line which passes between the calcaneum and cuboid. This derived arrangement necessitated the elimination of the cuboid pivot, as this would inhibit extensive dorsoplantar movements of the forefoot. As the requirements for mediolateral rotations diminished and as forces incurred from the substrate would require a calcaneocuboid joint with increased freedom of movement in a dorsoplantar direction, one would expect the pivot to be reduced or diminished. Under what arboreal locomotor circumstances would a lesser frequency of mediolateral rotations and increased flexion-extension movements be required? If the arboreal substrate could be reached between two stances of the animal with a recurring regularity of orientation of this substrate then the above modification of the pes could be of increased mechanical advantage. Vertical stems as opposed to the branches (which are discontinuous, curved, mobile, and variably oriented to the pull of gravity) would require less varied foot orientation for an animal moving in such a habitat. Thus, this particular feature of *Tarsius* is an adaptation to grasp, rest, and push off from vertically oriented branches or trunks of plants. No such adaptations are known among the vertical clinging and leaping strepsirhines. If the series of inferences presented here from morphology to function and from the latter to biological role are correct then the morphology associated with vertical clinging and leaping, at least in *Tarsius*, is clearly advanced when compared with primitive omomyids, lemuriforms, or the paromomyiforms.



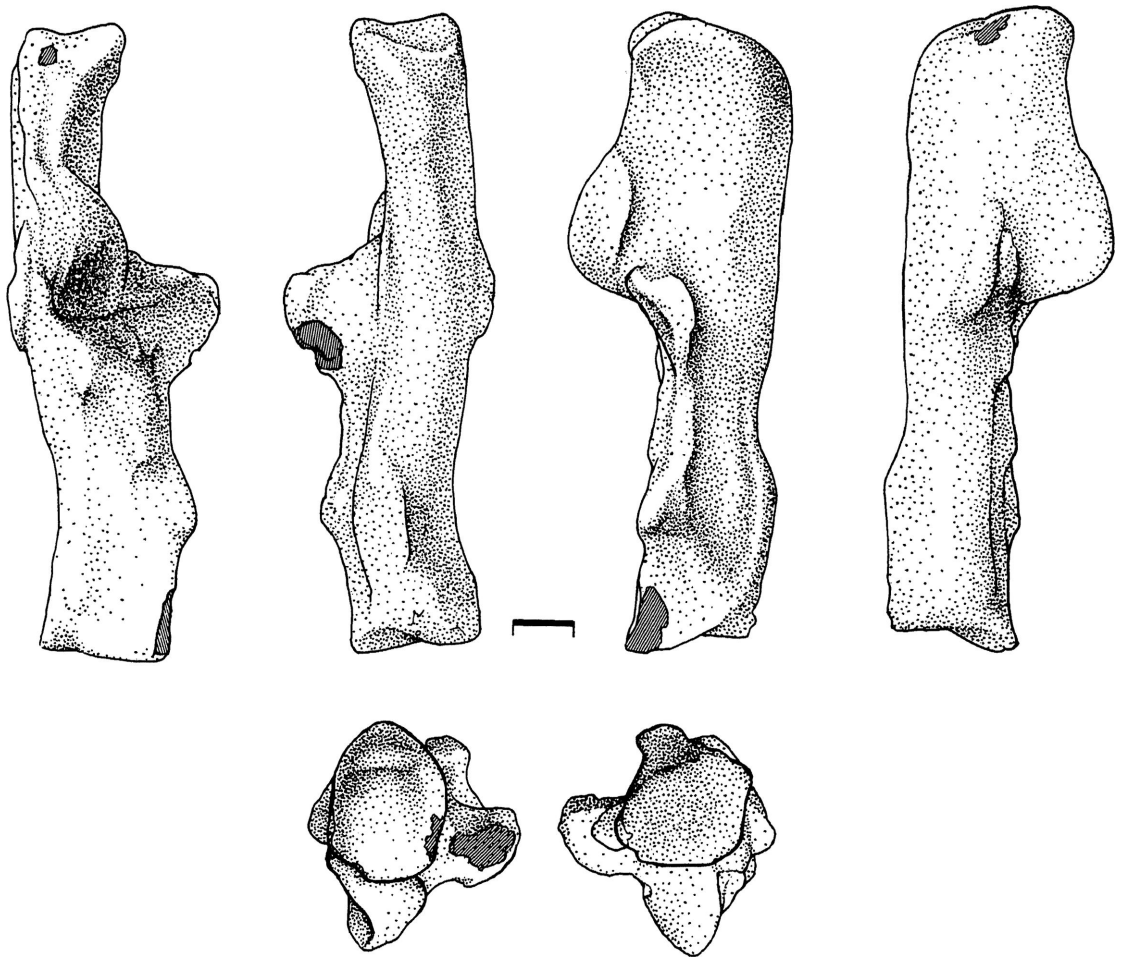


FIG. 163. Omomyine B, based on AMNH 88824 from Bridger beds, Bridgerian (medial Eocene), right calcaneum; from left to right first and second rows: dorsal, ventral, medial, lateral, proximal, and distal views. Scale represents 1 mm.

FIG. 162. Anaptomorphine, probably *Tetonius homunculus*, East Alheit Pocket, Wasatchian (early Eocene), right calcaneum (above), based on AMNH 8820, 8821, and 8823; right astragalus (below), based on AMNH 88817 and 88818; from left to right first and second rows: dorsal, ventral, medial, lateral, proximal, and distal views. Scales represent 1 mm.

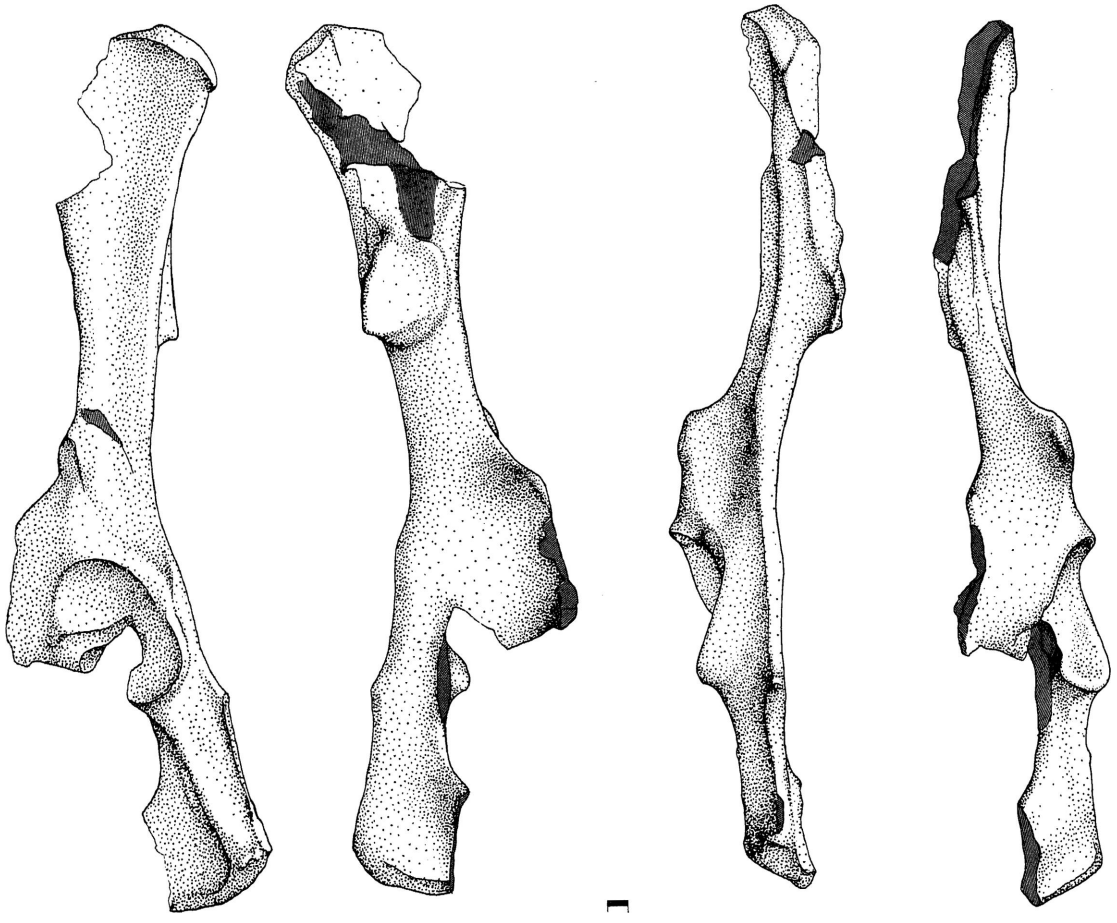
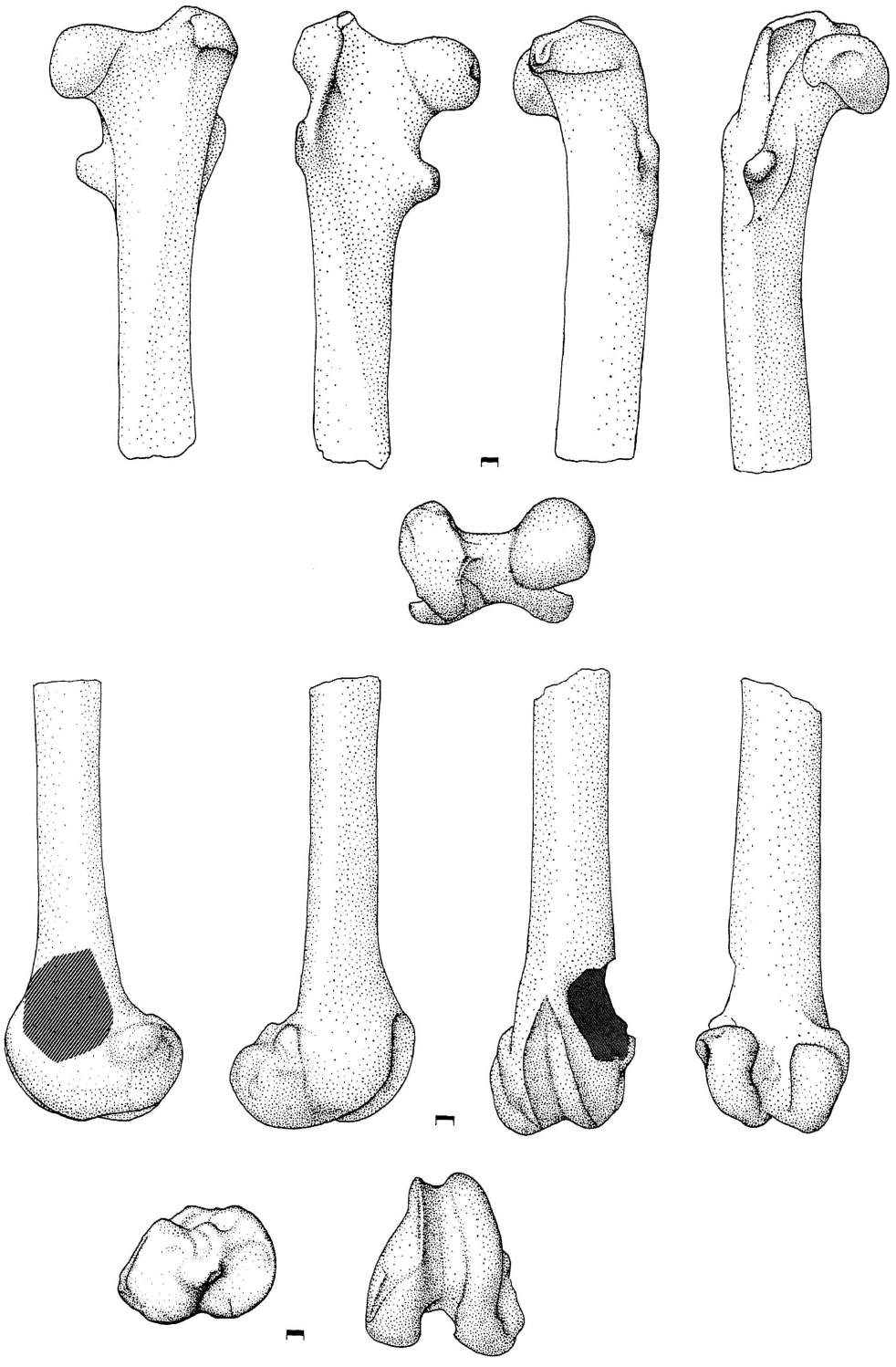


FIG. 164. *Hemiacodon gracilis*, AMNH 12613, Bridger beds, Bridgerian (medial Eocene), broken left pelvis; from left to right: lateral, medial, dorsal, and ventral views. Scale represents 1 mm.

FIG. 165. *Hemiacodon gracilis*, AMNH 12613, Bridger beds, Bridgerian (medial Eocene), broken left femoral fragments (proximal end above and distal end below) and proximal view of left tibia (below left); from left to right above: anterior, posterior, lateral, medial, and dorsal views; from left to right below; medial, lateral, anterior, posterior, proximal (tibia), and distal views. Scales represent 1 mm.



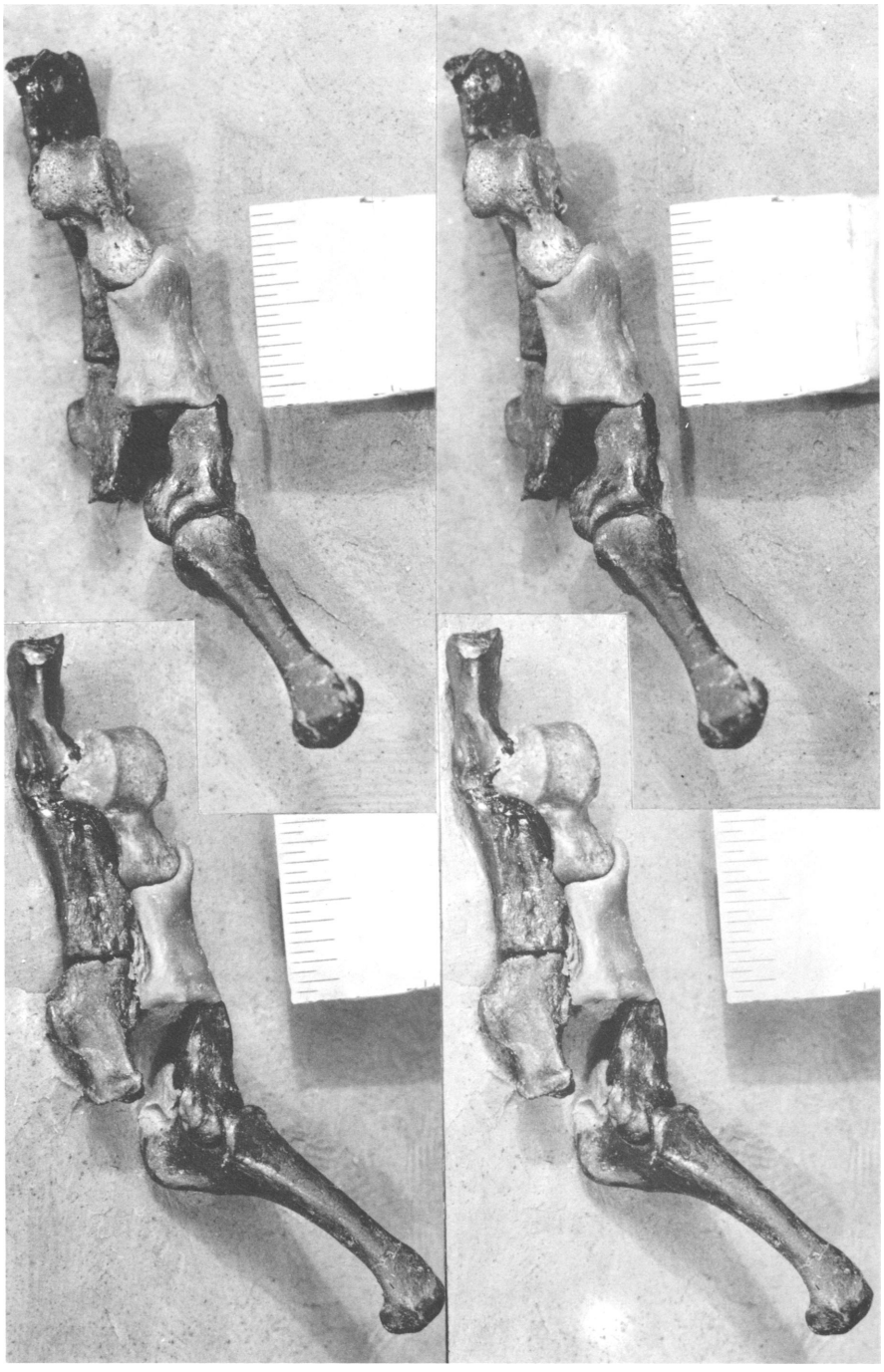


FIG. 166. *Hemiacodon gracilis*, composite of partial right foot. All, except astragalus and navicular, are AMNH 12613, Bridger beds. Stereophotographs: two different dorsal views. Subdivisions on scales represent 0.5 mm.

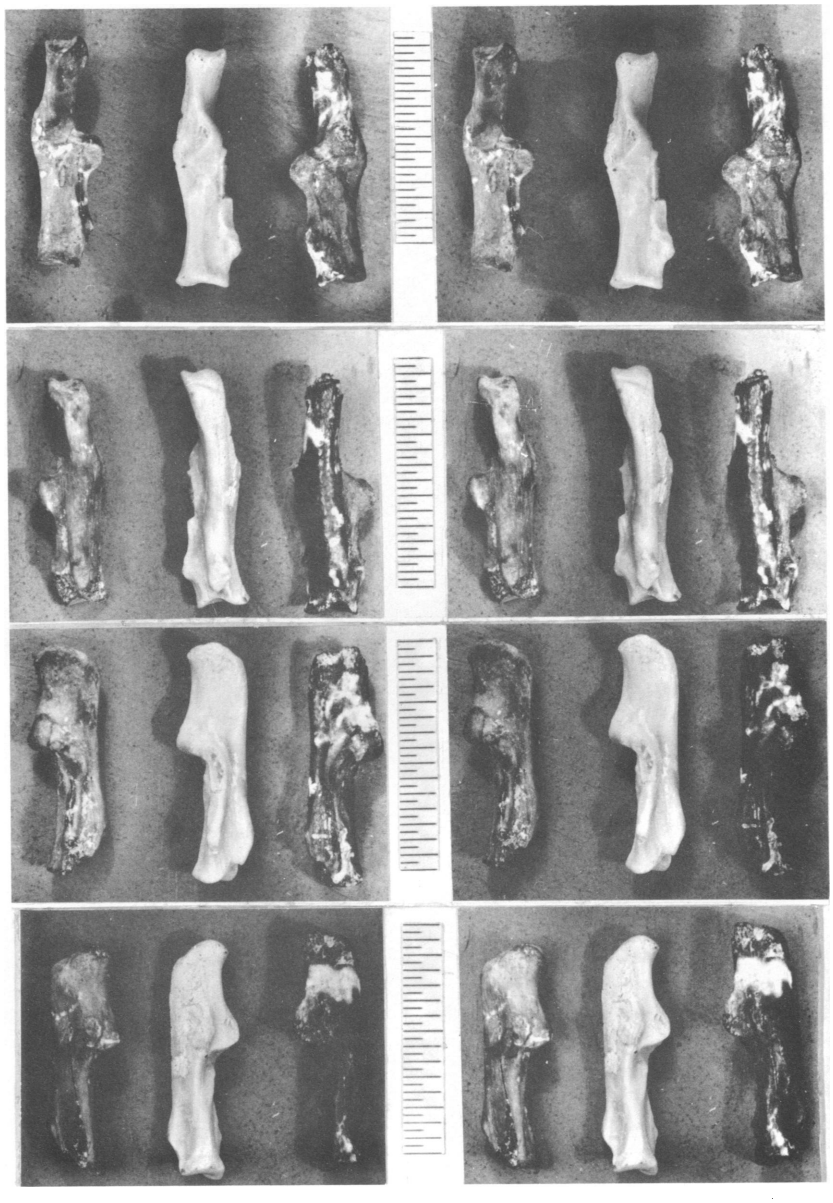


FIG. 167. *Hemiacodon gracilis*, YPM 24472 (left); YPM 24475 (middle); and YPM 24457 (right); all calcanea from Bridger beds. Stereophotographs: dorsal (above), ventral (above center), medial (below center), and lateral (below) views. Subdivisions on scales represent 0.5 mm.

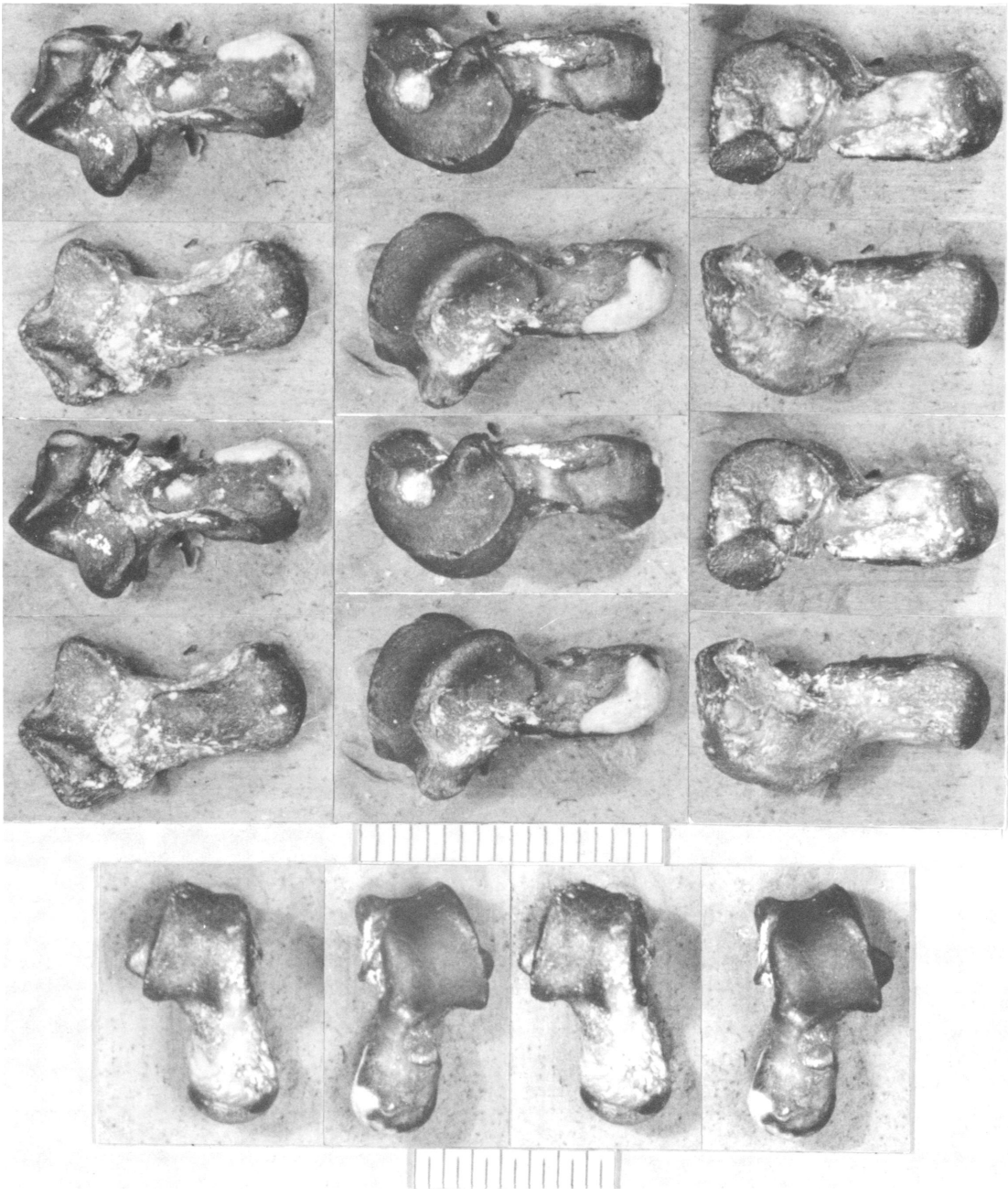


FIG. 168. *Hemiacodon gracilis*, YPM 24462, left astragalus (above and below right); YPM 24465, right astragalus (center and below left), both from Bridger beds. Stereophotographs: ventral (left), medial (middle center and right), lateral (top center and right), and dorsal (below) views. Subdivisions on scales represent 0.5 mm.

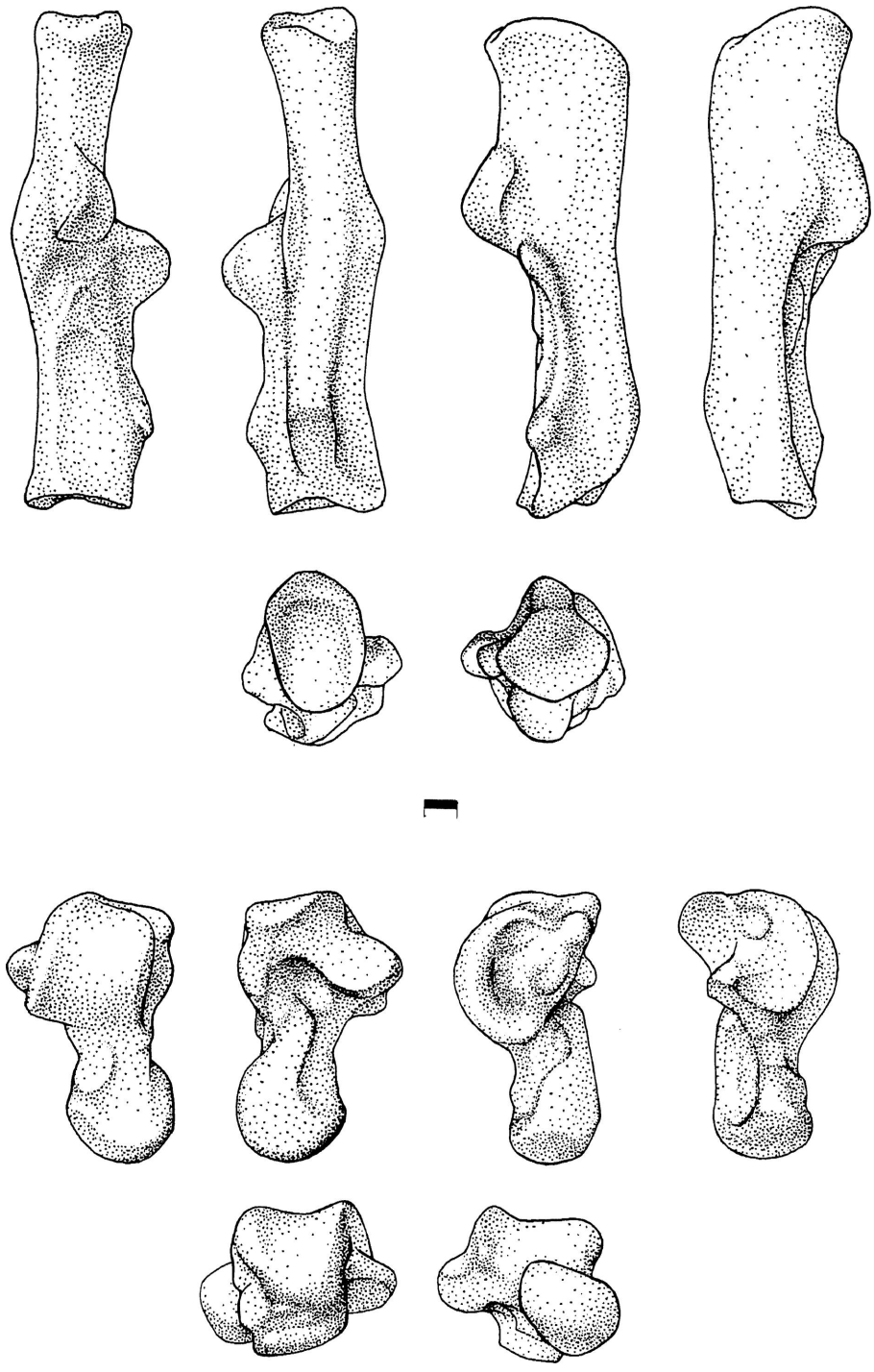


FIG. 169. *Hemiacodon gracilis*, right calcaneum (above) and right astragalus (below), based on several specimens from Bridger beds; from left to right dorsal, ventral, medial, lateral, proximal, and distal views. Scale represents 1 mm.

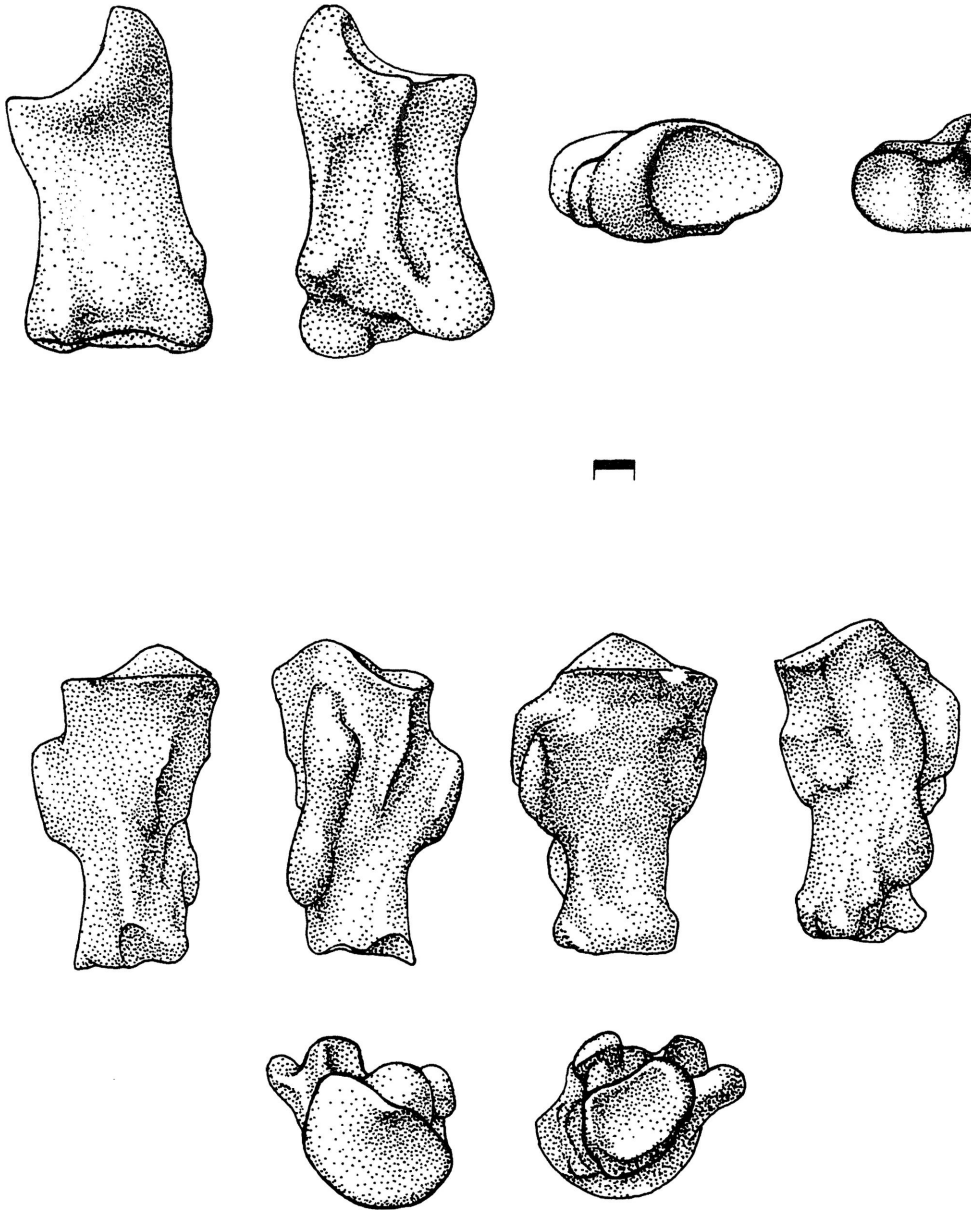
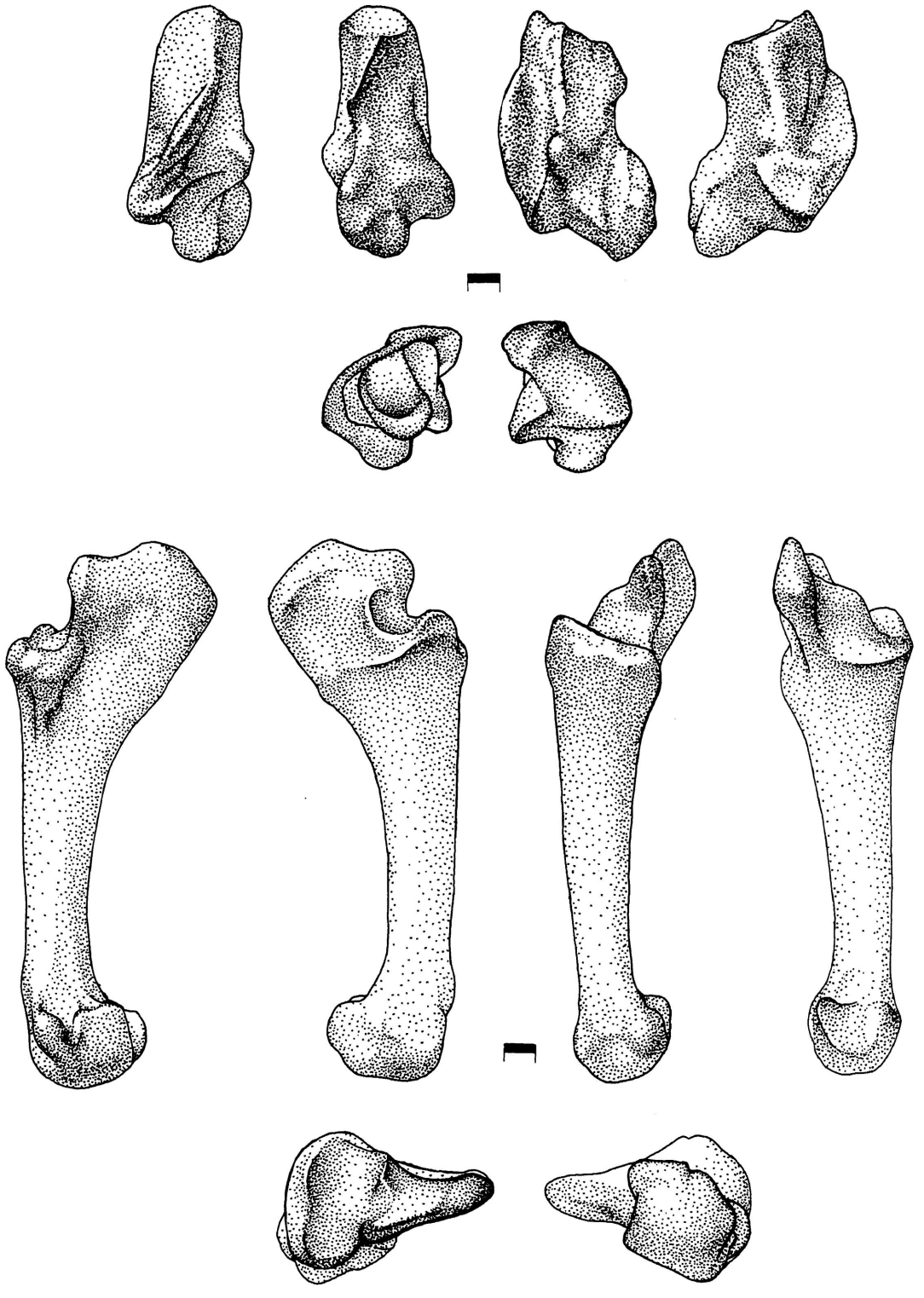


FIG. 170. *Hemiacodon gracilis*, right navicular (above) and right cuboid (below), based primarily on AMNH 12613, Bridger beds; from left to right: dorsal, ventral, proximal, and distal views of the navicular; from left to right: dorsal, ventral, lateral, medial, proximal, and distal views of the cuboid. Scale represents 1 mm.

FIG. 171. *Hemiacodon gracilis*, AMNH 12613, Bridger beds, right entocuneiform (above) and first right metatarsal (below); entocuneiform from left to right: ventral, dorsal, lateral, medial, proximal, and distal views; first metatarsal from left to right: ventral, dorsal, lateral, medial, proximal, and distal views. Scales represent 1 mm.



roneal tubercle, although clearly more advanced than the condition in paromomyiforms, is more primitive than the absence of this process in known omomyids.

The movements at the lower ankle joint are well reflected on the posterior astragalocalcaneal facet and, of course, also on the calcaneoastragalar facet. Omomyids, adapids, and paromomyiforms show what Szalay and Decker (1973) described as a recurved posterior astragalocalcaneal facet, suggesting a screwlike rotation at the lower ankle joint. As previously pointed out by Hall-Craggs (1965) this arrangement increases the potential range of this joint, effecting inversion and eversion. As no meaningful differences exist between the three groups and most other known primates this condition of the lower ankle joint is almost certainly primitive for the order.

The relevance of the African Miocene lorisiform calcanea recently reported by Walker (1970) must be discussed at this point. I have compared the lorisoid calcanea from Songhor to those of omomyids, adapids, lemuroids, and extant lorisids. These bones, when first reported by Walker (1970), were correctly distinguished as belonging to three different species. These three forms are represented by KNM SGR 2094, SGR 2010 and SGR 2556. The drawings presented by Walker (1970, fig. 8) are somewhat simplified and in particular the size differences shown between KNM SGR 2010 and KNM SGR 2556 are not as shown by his figure. The specimens are shown in figures 172 and 173. In discussing these bones Walker noted (p. 253), "The shape of the fossil calcanea, apart from the lesser distal elongation, compares closely with those of modern galagos even to the extent of having a joint surface showing the presence of an anterior calcaneonavicular synovial joint as described by Hall-Craggs ('66)." I cannot ascertain the presence of a well-developed and distally displaced calcaneonavicular joint, as in galagos, and I find no other shared derived similarities between the calcanea of living galagos and the fossils. Any one of them, on the other hand, is ideal to pass for a structural ancestor for the calcaneum of lorises and galagos. Rather than sharing special similarities with galagos, the Miocene calcanea are primitive lorisoid and thus astonishingly similar to those of such cheirogaleids as *Cheirogaleus* and *Phaner*.

Similarity between the Miocene calcanea and those of known omomyids, excluding that of *Necrolemur*, is great. I suspect, however, that this similarity is due partly to both having aspects of primitive morphology, that of a lemuriform ancestor, and due to independent acquisitions, i.e., the distal elongation of the calcaneum.

The relative forces transmitted between the astragalus and navicular during either inversion or eversion are well reflected on the head of the astragalus. The reasons for such conclusions have been discussed in detail by Szalay and Decker (1973) and will not be repeated here. Comparisons of omomyid astragalar heads with adapids and paromomyiforms reveals a significantly advanced condition. The medial side of the head is absolutely thicker in some than the lateral one and it is perhaps relatively thicker than those of adapids. This indicates an increase in the forces transmitted during inversion over the more primitive primate condition. Interpreting this fact by suggesting a "more arboreal" substrate preference for omomyids than adapids, for example, makes little sense. It appears, however, that the rest phase of the stance in omomyids might have required a habitually more inverted foot position than required of most fully arboreal quadrupeds. The resting position of a habitual leaper might explain the mechanical requirements reflected on the astragalar head.

The upper ankle joint, as shown by the body of the astragalus and the distally fused tibia and fibula of *Necrolemur* and *Nannopithex*, was significantly different in omomyids compared with those of adapids and paromomyiforms. Many lemuriforms retain at least the dorsal foramen leading into the astragalar canal. However, no known omomyid astragali show traces of this canal which is clearly primitive for the Eutheria and apparently also present in the ancestral Primates and some Malagasy lemuriforms.

The body of the astragalus of *Teilhardina* shows a posterior extension which may be considered homologous to the posterior trochlear shelf of adapids described by Decker and Szalay (1973). As this feature is best developed in *Teilhardina*, but not recognizable unequivocally in

Hemiacodon or in ?*Tetonius*, its moderate expression in the European omomyid may reflect a feature retained from an ancestral condition which is judged to be lemuriform. The reduced condition or absence of this shelf (the semantics of description become very difficult as this is a continuous bony extension of the astragalar body) thus might represent an advanced character state in the remaining omomyids, compared with a primitive one in which the shelf was present. Thus the posterior trochlear shelf was likely to be present in the ancestor common to the taxa included in the Omomyidae.

In summarizing the tarsal evidence, it can be said that the majority of the character states known for omomyid calcanea and astragali appear to be derived ones when compared with their adapid homologues. Such features as the screw-type lower ankle joint are primitive for the whole order.

RELATIONSHIPS AND CLASSIFICATION WITHIN THE TARSIIFORMES

The classification of the Omomyidae, based on the criteria of an inferred phylogeny (fig. 138) and phenetic divergence, is presented in the systematic section and an overview can be attained in the Table of Contents. I consider the groupings among and within the Anaptomorphinae, Omomyinae, Ekgmowechashalinae, and Microchoerinae balanced and comparable with the equivalent subdivisions within the Paromomyiformes, Strepsirhini, Platyrrhini, and Catarrhini.

The Microchoerinae, probably best classified at present as a subfamily of the Omomyidae, has not been revised. Preliminary studies of my own, but particularly that of Russell, Louis, and Savage (1967), indicate *Nannopithex*, *Necrolemur* (figure 149), *Microchoerus*, and *Pseudoloris* (figures 150-152) to be the valid genera in this group. The only features that might separate these from other omomyids (and it is doubtful that these are only microchoerine characters) involve some advanced character states such as distal tibio-fibular fusion, and the previously noted extreme inflation of the mastoid. It is possible that the considerably enlarged first lower incisor is a primitive feature of the Microchoerinae.

Whether tibiofibular fusion is homologous to that of tarsiids or if it occurs in omomyines and anaptomorphines is unknown. There are a number of outstanding cranial differences between the extant *Tarsius* spp. (figure 145) and *Necrolemur antiquus* (figure 144) which supply strong arguments against classification of these taxa in the same family and therefore they are discussed above. As noted, the comparison revealed some highly derived conditions of the basicranium in the extant genus but not in the European form, and vice versa. Dorsal and anteromedial to the promontorium of *Tarsius* a diverticulum, an air space, is enormously enlarged and this is strikingly reflected in the very large anteromedial segment of the bulla. In *Necrolemur* this section of the bulla is undeveloped, although a middle ear diverticulum is present. The skull of *Tetonius* is poorly known, yet there are indications on the generotype that suggest a condition not unlike that found in *Necrolemur*. In spite of what is usually stated or implied, petromastoid inflation is minimal or virtually nonexistent in *Tarsius*. There are three major dome-shaped enlargements on the occiput, as in *Necrolemur*. These seem to be contoured to the shape of the two lateral lobes and the vermis cerebelli of the cerebellum. *Necrolemur*, however, has an enormously enlarged petromastoid. As there is no evidence that this uninflated petromastoid of *Tarsius* is secondary, the condition of this area in *Necrolemur* almost certainly appears to be the more derived character state. The crushed skull of *Tetonius* suggests a petromastoid very much like that of *Necrolemur*, a character of some significance in the assessment of its relative phyletic position. *Rooneyia* (figure 143), however, shows no excessive inflation of the petromastoid. The petromastoids of *Rooneyia* and *Tarsius* are then either mere symplesiomorphies and therefore should not be used to signify special ties between these two genera, or, as a remote possibility, a convergently derived condition in these two forms. As noted above, pronounced inflation of the mastoid was probably present in the anthropoid morphotype, although in the common haplorhine ancestor it was probably uninflated.

The discussion in the section on phylogen' and classification is pertinent to both the rel

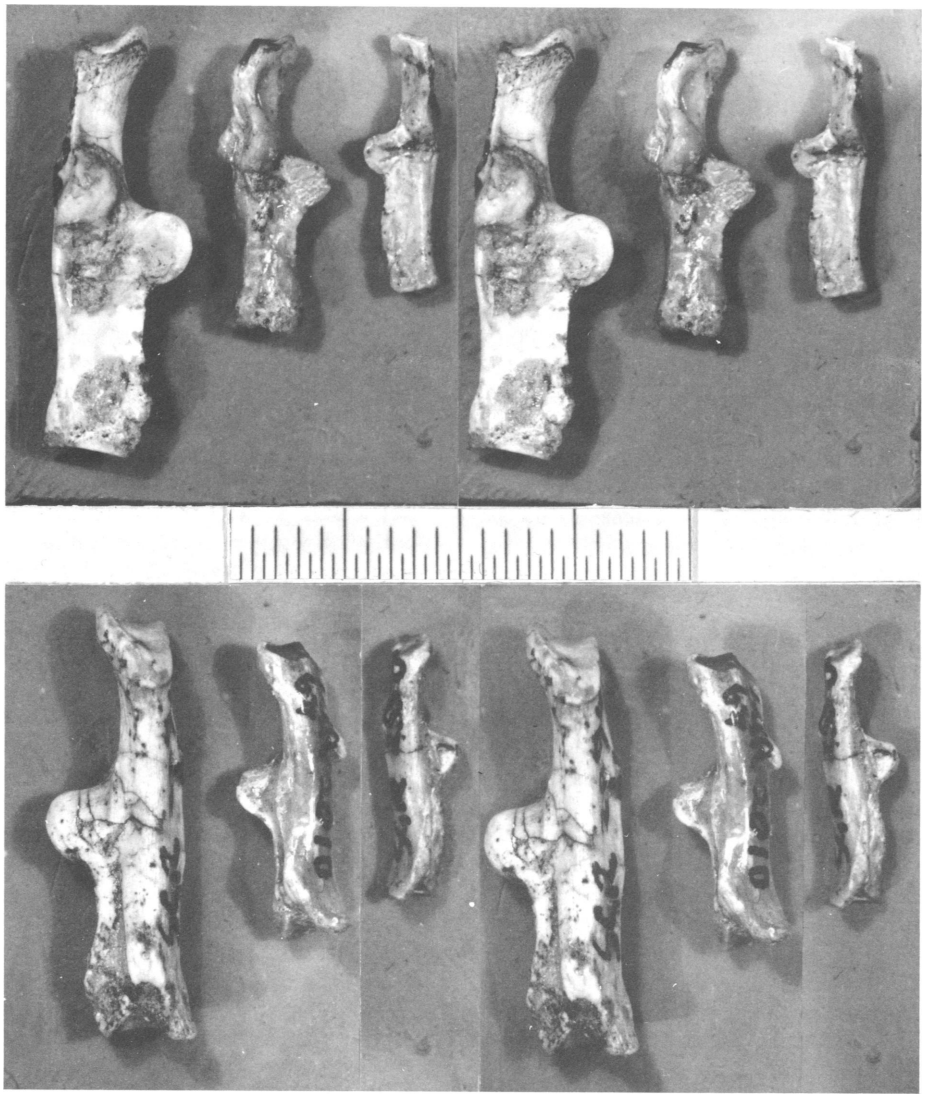


FIG. 172. Songhor Miocene lorisid calcanea, KNM S2094, right calcaneum (left); KNM S2010, right calcaneum (center); and KNM S2550, left calcaneum (right), all from Kenya, East Africa. Stereophotographs: dorsal (above) and plantar (middle), views. Subdivisions on scale represent 0.5 mm.

tionships and taxonomic status of the Microchoerinae.

A historical review of the phylogenetic ties and classification of *Tarsius* was presented in detail by Jones (1929, pp. 165-174). Jones, like Gadow, Hubrecht, and others before him, strongly argued for the closer affinities of *Tarsius* with catarrhines and platyrrhines rather than with any of the strepsirhines. In comparing the morphology of *Tarsius* with that of omomyids, platyrrhines, and catarrhines several problems of phylogeny and subsequently classification are solved but new questions are posed. I am confident in the unity of the omomyids, tarsiids,

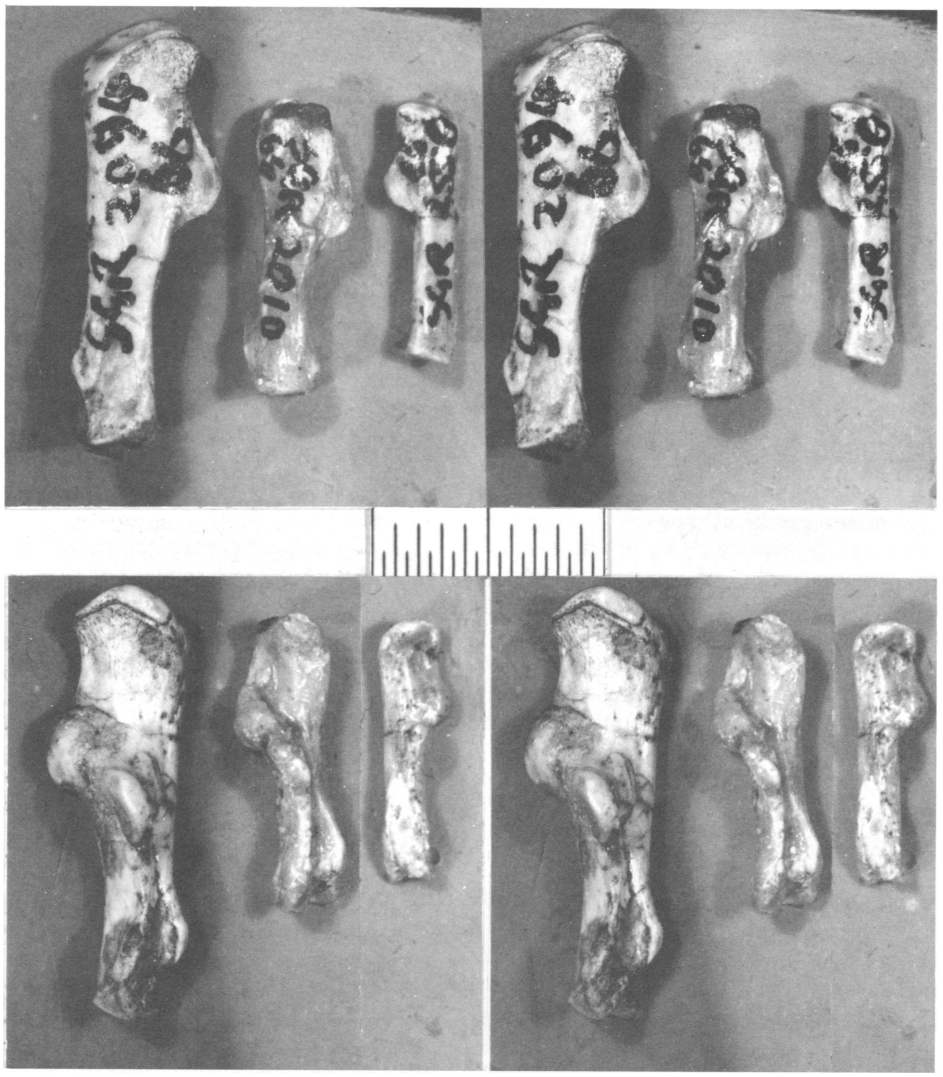


FIG. 173. Songhor Miocene lorisid calcanea, KNM S2094, right calcaneum (left); KNM S2010, right calcaneum (center); and KNM S2550, left calcaneum (right), all from Kenya, East Africa. Stereophotographs: lateral (above) and medial (below) views. Subdivisions on scale represent 0.5 mm.

platyrrhines, and catarrhines; they most likely share a common ancestor, a haplorhine that diverged from a lemuriform stock. Taking the four haplorhine groups together, however, it is difficult at present to determine relative recency of common ancestry between these four natural groups. It seems possible that platyrrhines arose from omomyine omomyids (but see below). *Tarsius*, considering its unusual bullar specializations, its enlarged promontory artery, and the tarsal structure, is best derived from an ancestry that may be called a primitive omomyid stock, but probably not a microchoerine (see discussion on microchoerine-tarsiid differences). In light of the numerous derived features of *Tarsius* and the inferred structural common ancestor of all omo-

myids it is much more meaningful to place the common ancestor of omomyids and *Tarsius* in the Omomyidae.

Questions of importance and of considerable difficulty concern the inferred ancestral condition of the platyrrhine and catarrhine astragalocalcaneal complexes and the nature of the tibia and fibula in the primitive omomyid condition. Was the primitive condition in the former two higher categories likely to have been as that shown in known tarsals of omomyids or do they suggest derivation from a foot and crus with a less derived character complex than that of known omomyids? Did primitive omomyids have a fused tibia and fibula? Answers to these questions will eventually lead to such problems as the existence of a group of primates tarsally more similar to platyrrhines, although referred to as tarsiiforms, not possessing some of the derived character states of either of the two tarsiiform families. Continued recovery of new fossils, attention to fragmentary postcranial remains, and intense evolutionary morphological studies (not exclusively from either the traditional taxonomic or functional points of view but rather from a combination of the two approaches) of platyrrhines and catarrhines will bring us closer to solving these problems.

It is difficult to establish for all known parts of the anatomy whether omomyids are phenetically more like the tarsiids or the morphotype of the platyrrhines. No primitive tarsiids are known, and although the omomyids are relatively poorly known both cranially and postcranially, it appears to me that the primitive tarsiid condition is best considered to have been well within the range of variation recognized for the Omomyidae. Many omomyids may have shared a more recent common ancestor with the common ancestor of both platyrrhines and catarrhines than with the ancestral tarsiids. In spite of this phyletic possibility it is more advisable, based on the overall morphology of the omomyids, to allocate the Omomyidae to the Tarsiiformes.

RELATIONSHIPS AND CLASSIFICATION WITHIN THE HAPLORHINI

I will examine some of the evidence for the hypothesis that there is a more recent common ancestry between tarsiiforms, platyrrhines, and catarrhines than between any of the three groups and any strepsirhine or paromomyiform primates. Perhaps one of the more convincing character complexes that allows the best use of fossils for phylogenetic inference on the level of mammalian higher categories is the morphology of the basicranium. It is complex and often conservative within family groups, yet often divergent enough between families and superfamilies, as noted above. As reported above and elsewhere (Szalay and Katz, 1973), basicranial morphology reveals a dichotomy between the strepsirhine and haplorhine morphotypes at least in a number of closely interwoven characters, e.g., the nature of the bulla and the relative size and path of the internal carotid branches and the various orifices associated with them.

A gap exists between the tarsiiform morphotype and what can be judged the more primitive basicrania of known anthropoids. Considering the tarsiiform evidence, the most primitive living anthropoid basicranial morphology appears to be possessed by the cebids, forms relatively conservative among themselves in this respect. Nevertheless, a detailed survey of the anthropoids would greatly aid determination of possibly significant morphocline polarities among platyrrhines and catarrhines.

Until now, fossil anthropoid basicrania have been largely lacking. Recently, however, important evidence with bearing on ancestral anthropoid morphology has been described by Gingerich (1973). The right petrosal and squamosal (YPM 23968) reported by him are allocated to *Apidium phiomense* from the Upper Fossil Wood zone of the Jebel el Quatrani Formation. In addition to describing the specimen (1973), Gingerich (1974) has formalized his views by erecting the suborder Plesitarsioidea to show the special ties of archaic, nonlemuriform primates with the tarsiiforms, and the Anthrolemuroidea to suggest the origin of the Anthropoidea from a lemuriform rather than a tarsiiform stock. His arguments for the validity of the lemuriform-anthropoid tie (Gingerich, 1973) are as follows: (1) characters of soft anatomy are not known from fossils and therefore it is nearly impossible to tell whether suggested haplorhine similarities are synapomorphies, merely primate symple-

siomorphies, or independently acquired characters: hence soft anatomical features bearing on haplorhine monophyly can be dismissed; (2) only osteological characters should be used to test the validity of the Haplorhini; (3) there is no evidence for any derived osteological features shared by *Tarsius* and anthropoids that can be shown to be due to common inheritance; (4) postorbital closure in *Tarsius* is different from anthropoids; the promontory arteries of primitive lemuroids are not so relatively small as has been reported hence the diagnostic differences between the carotid circulation of living lemuroids and *Tarsius* were not as yet established by the medial Eocene; (5) presence of a free ectotympanic in tupaiids proves that the primitive primate condition of the bone was as seen in lemuroids; (6) because *Necrolemur* and *Rooneyia* are widely separated geographically and morphologically, a tubular ectotympanic was an early acquisition of tarsiiforms; (7) early catarrhines and platyrrhines lack a tubular ectotympanic; hence anthropoids were derived from primates more primitive than any known tarsioids; (8) "*Apidium* provides positive evidence that anthropoid primates evolved directly from a lemuroid ancestor" (p. 335); (9) because *Pelycodus* and close relatives can be found during the early Eocene in both North America and Europe, the distribution pattern of anthropoids does not require rafting hypotheses.

It is emphasized in the following assessment of the views and arguments expressed by Gingerich, that I cannot corroborate his proposed primate phylogeny. His hypothesis, incidentally, is not unlike the one proposed by Saban (1963, p. 333, fig. 84). (1) and (2). Numerous, if not all, osteological characters are mechanically linked to soft anatomy, and therefore soft anatomical characters cannot be rejected for phyletics. The great diversity of many soft anatomical features allows construction of more extensive morphocline polarities than usually permitted by the available fossils, a fact favorably balancing their absence in the fossil record. (3). Lack of osteological (but not soft anatomical!) synapomorphies between *Tarsius* and anthropoids is no argument against inferred synapomorphies between the most recent relatives of *Tarsius* (e.g., omomyids, or their morphotype) and the common ancestor of platyrrhines and catarrhines. (4). An assessment of the relative sizes of the stapedial artery in *Pelycodus* sp. and *Necrolemur antiquus* (see above) indicates, contra Gingerich, that at least in these taxa, after the subdivision of the lateral carotid artery, the stapedial canal is emphasized in the former and the promontory one in the latter. In these two lineages the differences were likely to have been established prior to the early Eocene. (5). A free intrabullar ectotympanic in tupaiids does not prove or disprove that this condition was present in the primate morphotype. (6). A tubular ectotympanic on the outside of the petrosal is clearly present in known tarsiiforms, but this cannot be causally linked with the three distinct stages displayed by the intrabullar portions of the ectotympanic and ossified annulus membrane in *Rooneyia*, *Necrolemur*, and *Tarsius*. In *Tarsius*, the tarsiiform ectotympanic is in its most derived condition, closely juxtaposed against the lateral wall of the bulla. A condition similar to this without a wide extrabullar component is essentially the one we find in platyrrhines. Both *Apidium* and *Aegyptopithecus*, unlike later cercopithecoids and hominids, have a platyrrhine-like ring rather than a tube. (7). The ringlike ectotympanic may have been primitive for the anthropoids, and, as argued under (6), this configuration was probably present in bona fide, advanced tarsiiforms. Lorisids show the fully differentiated features of their family, inherited from a cheirogaleid diverged from a lemuroid ancestry, yet they display a variety of conformations of the ectotympanic (contrast *Galago* vs. *Nycticebus*, for example). This character, as noted, is apparently quite independent from major alterations in the circulatory pattern or the degree of petromastoid inflation. (8). I cannot ascertain the positive evidence for anthropoid origins directly from the lemuroids. There are, I believe, a few incorrect observations in Gingerich's description; consequently, his only evidence for relating the *Apidium* basicranium to lemuroids appears to be of doubtful significance. The broken posterior crus of the ectotympanic is probably correctly identified, but a small depression he asserts to be a facet for the anterior crus may or may not be for the ectotympanic. The anterior crus probably fitted immediately medial

to the postglenoid process into a discernible groove that extended posteriorly medial to the postglenoid foramen. This is exactly what one finds in many specimens of platyrrhines like *Saimiri.* The lack of fusion of the anterior crus would not be unexpected in a relatively young individual. In addition, information on the extent of fusion in the early tarsiiforms is lacking.[1] (9). The statement that the presence of *Pelycodus* in Europe and North America does not suggest dispersal of early anthropoids from either Africa or South America implies that (a) *Pelycodus* is the common ancestor of the Anthropoidea, and (b) the Platyrrhini and Catarrhini independently evolved a number of shared characters clearly not present in *Pelycodus.* I consider the evidence nonexistent and therefore this phylogenetic conclusion fallacious.

The evidence from the petrosal of *Apidium* is important for both cladistic and anagenetic assessment of anthropoid origins. An anthropoid specialization, contrasted to those of other primates, is the extreme enlargement of the promontory artery. This vessel plunges into the petrosal quite medially and appears, in its probably primitive form, both in *Apidium* and some platyrrhines and catarrhines as a raised surface on the medial side of the promontorium (figure 147). Another character that appears to be a synapomorphy between *Apidium*, platyrrhines, and catarrhines is the pneumatized nature of both the petrosal and squamosal. This feature could link an anthropoid morphotype with a group of early tarsiiforms that had an enlarged petromastoid and an ectotympanic ring outside the bulla proper. Furthermore, the sinus-filled bullar portion of anthropoids (figure 147C-E) corresponds to the area in tarsiiforms, such as *Tarsius*, which usually has a large hypotympanic sinus.

[1]After this work had gone to press, Hershkovitz (1974) showed that the unfused anterior crus of the ectotympanic can be found not only in lemuriforms but also in immature *Tarsius* and in immature and even some mature individual cabids.

The tarsiiforms, platyrrhines, and catarrhines, in contrast to strepsirhines, share a distinctly enlarged promontory artery relative to the stapedial one derived from an adapid ancestor. The enlarged promontory artery is certainly a derived character in all three higher categories and it is most likely a shared derived condition from a common ancestry rather than a convergent one. In addition to the basicranial morphology, discussed below, the morphocline polarity of the early development of the fetal membranes of primates (Luckett, 1971, 1974) is equally convincing in showing that *Tarsius* shares derived developmental patterns with platyrrhines and catarrhines but not with strepsirhines.

Among the Haplorhini the inferred common ancestor of the Tarsiiformes is distinctly more primitive than those of either the Platyrrhini or Catarrhini. The problem of the nature of the genealogical relationships of the last two and the biogeographical aspect of their evolutionary history are still unresolved. Some of the questions concerning the Anthropoidea, however, may be asked as follows. Are the morphotypes of known platyrrhines and catarrhines more recently related to each other than either of them to taxa that we would classify as tarsiiforms? Or, are the primitive platyrrhine and primitive catarrhine character states shared derived features, or were they convergently (=parallel) derived from a tarsiiform level of organization, something, perhaps, akin to that displayed by *Rooneyia*? In other words, was there a stock of primates that possessed the "simian-grade of organization," the characters listed below, and were these common ancestors of the platyrrhines and catarrhines? Stated this way the problem is perhaps a little clearer than the usual question whether South American "monkeys" are "true" monkeys or not (see also Hoffstetter, 1972, and Hershkovitz, 1969).

There is no space here to examine what this simian grade might be but it may be summarized as usually understood to mean a combination of convergent, perhaps frontated orbits, orbital funnels (i.e., postorbital closure), frontal suture fu-

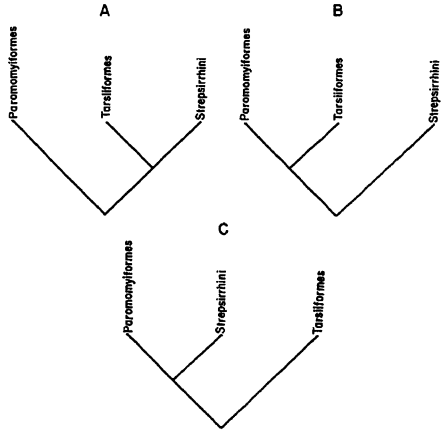


FIG. 174. Three cladograms showing three different hypotheses for genealogical relationships of the Paromomyiformes, Strepsirhini, and Tarsiiformes, from the most probable (A) to the least likely (C).

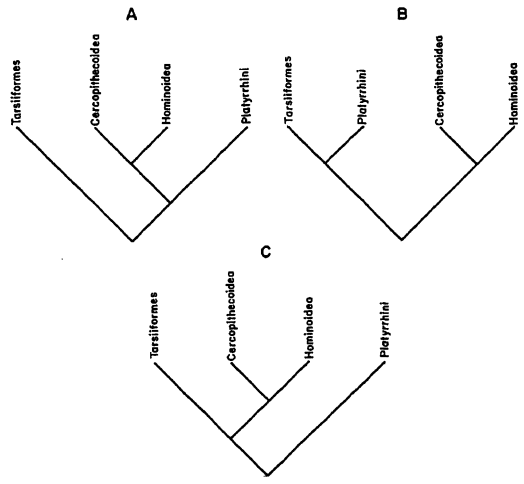


FIG. 175. Three cladograms showing three different hypotheses for genealogical relationships of the Tarsiiformes, Platyrrhini, and Catarrhini (Cercopithecoidea and Hominoidea), from the most probable (A) to the least likely (C).

sion at an early age, synostosed mandibular symphysis, an enlarged brain with specific sulcal patterns, a pneumatized bulla, and a very large promontory branch of the internal carotid.

This primarily phylogenetic problem may be broken down into two general ones, the first dealing with the nature of genealogical relationships between the known Haplorhini and the other with the known facts needed to determine these relationships. The aim is, clearly, to determine which of the three phylogenetic hypotheses, presented in figure 175 is the most plausible. Given the more recent common ancestry of the Hominoidea and Cercopithecoidea than that of either with any of the other known haplorhines the three cladograms cover all the possibilities of genealogical ties among the three infraordinal categories of the Haplorhini. The manner in which the three genealogical hypotheses are presented are not meant to imply three different judgments of anagenesis but are merely a statement on the recency of relationships. Figure 175A shows the Anthropoidea (*sensu* Mivart, 1873, and Simpson, 1945) to be a monophyletic category, whereas figure 175B and C do not. The three hypotheses differ from each other in the relative recency of a common ancestor between the Tarsiiformes, Platyrrhini, and Catarrhini. The evidence is overwhelmingly in favor of A, B is not impossible, and C is rather unlikely.

Considerations advanced here are tied to osteological evidence of the haplorhines because comparative analysis that involves the fossil groups is restricted to the skeletal system. Lack of Tertiary tarsiiform soft anatomy or biochemical attributes makes it difficult to judge which states of these characters of living haplorhines are primitive haplorhine, platyrrhine, catarrhine, or truly anthropoid in nature. Clearly, however, careful and broadly comparative studies on all living primates can surmount these obstacles, and the wealth of usable characters in extant species, as noted above, balances the lack of "soft" features in the fossil record.

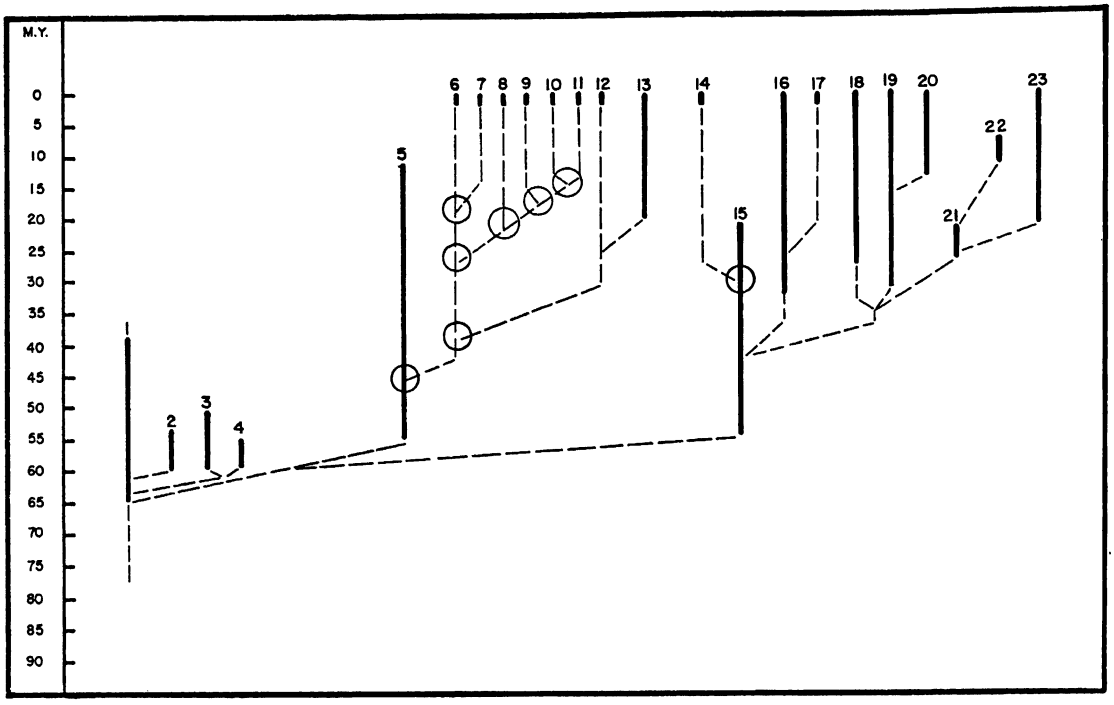


FIG. 176. Suggested phylogenetic relationships of the recognized families of primates. Solid heavy lines represent known ranges and broken lines depict recency of relationships. 1. Paromomyidae; 2. Picrodontidae; 3. Plesiadapidae; 4. Carpolestidae; 5. Adapidae; 6. Lemuridae; 7. Megaladapidae; 8. Archaeolemuridae; 9. Palaeopropithecidae; 10. Daubentoniidae; 11. Indriidae; 12. Cheirogaleidae; 13. Lorisidae; 14. Tarsiidae; 15. Omomyidae; 16. Cebidae; 17. Callithricidae; 18. Hylobatidae; 19. Pongidae; 20. Hominidae; 21. Parapithecidae; 22. Oreopithecidae; 23. Cercopithecidae. Circles represent uncertainty as to even an approximate time of divergence.

TABLE 28

An Evolutionary Classification of Primates Based on a Phylogenetic Hypothesis Presented on Figure 176 and on a Compromise Judgment of Structurally Most Significant Differences between the Taxa

Order Primates Linnaeus, 1758
- Suborder Paromomyiformes Szalay, 1973
  - Superfamily Paromomyoidea Simpson, 1940
    - Family Paromomyidae Simpson, 1940
    - Family Picrodontidae Simpson, 1937
  - Superfamily Plesiadapoidea Trouessart, 1897
    - Family Plesiadapidae Trouessart, 1897
      - Subfamily Plesiadapinae Trouessart, 1897
      - Subfamily Saxonellinae D. E. Russell, 1964
    - Family Carpolestidae Simpson, 1935
- Suborder Strepsirhini E. Geoffroy, 1812
  - Infraorder Lemuriformes Gregory, 1915
    - Superfamily Adapoidea Trouessart, 1879
      - Family Adapidae Trouessart, 1879
        - Subfamily Adapinae Trouessart, 1879
        - Subfamily Notharctinae Trouessart, 1879

TABLE 28–(*Continued*)

Superfamily Lemuroidea Gray, 1821
Family Lemuridae Gray, 1821
Family Megaladapidae Flower and Lydekker, 1891
Superfamily Indrioidea Burnett, 1828
Family Indriidae Burnett, 1828
Family Archaeolemuridae Forsyth-Major, 1896
Family Palaeopropithecidae Tattersall, 1973
Family Daubentoniidae Gray, 1821
Infraorder Lorisiformes Gregory, 1915
Superfamily Lorisoidea Gray, 1821
Family Cheirogaleidae Gray, 1870
Family Lorisidae Gray, 1821
Subfamily Lorisinae Gray, 1821
Subfamily Galaginae Gray, 1825
Suborder Haplorhini Pocock, 1818
Infraorder Tarsiiformes Gregory, 1915
Family Tarsiidae Gray, 1825
Family Omomyidae Trouessart, 1879
Subfamily Omomyinae Trouessart, 1879
Subfamily Anaptomorphinae Cope, 1883
Subfamily Ekgmowechashalinae, new
Subfamily Microchoerinae Lydekker, 1887
Infraorder Platyrrhini Hemprick, 1820
Family Cebidae Bonaparte, 1831
Subfamily Cebinae Mivart, 1865
Subfamily Aotinae Elliot, 1913
Subfamily Pithecinae Mivart, 1865
Subfamily Atelinae Miller, 1924
Subfamily Alouattinae Elliot, 1904
Subfamily Xenothricinae Hershkovitz, 1970
Family Callithricidae Gray, 1821
Subfamily Callithricinae Gray, 1821
Subfamily Callimiconinae Thomas, 1913
Infraorder Catarrhini E. Geoffroy, 1812
Superfamily Hominoidea Gray, 1825
Family Hylobatidae Gray, 1870
Subfamily Hylobatinae Gray, 1870
Subfamily Pliopithecinae
Family Pongidae Elliot, 1913
Subfamily Ponginae Elliot, 1913
Subfamily Gigantopithecinae Gremiatskij, 1960
Family Hominidae Gray, 1825
Superfamily Cercopithecoidea Gray, 1821
Family Parapithecidae Schlosser, 1911
Family Cercopithecidae Gray, 1821
Subfamily Cercopithecinae Gray, 1821
Subfamily Colobinae Blyth, 1875
Family Oreopithecidae Schwalbe, 1915

PALEOZOOGEOGRAPHY

Past students of Mesozoic and Cenozoic vertebrates followed the status quo of the geological sciences of their times and have long held that the faunal distribution patterns can be explained based on essentially a stable late Mesozoic and Cenozoic continent distribution with the exception of occasional Bering-Alaska land connections. A stabilist view, held by geologists, paleontologists, and biologists until very recently was summed up in a symposium (Mayr, 1952). Most recent studies, however, have accepted a mobilist view of the earth's crust; the recent revolution in geophysics in regard to the wandering continental plates (continental drift) and subsequently wandering rotational poles is profoundly affecting not only interpretations of distribution, dispersal, and deployment of vertebrate faunas but its influence reaches the realm of phylogenetic interpretations as well (see Tarling and Runcorn, 1973).

The recent acceptance of continental drift carries with it a danger of "band wagon" mentality. In spite of the recent advances in the study of geological earth history, phyletic analyses of biological evidence should at first be as independently assessed as possible before attempts are made to decipher the paleozoogeography of a group. Only following the construction of phylogenies should one attempt to synthesize a sequence for the deployment of the known and postulated taxa.

No "final," comprehensive paleogeographical synthesis exists yet which would allow us to pinpoint the position of the major land masses and their proximities in given geological moments (but see Cracraft, 1973, and McKenna, 1973). Nevertheless attempting to reconstruct the adaptive radiation of any group of mammals without the existing pertinent geological and paleontological evidence is meaningless, even if the phylogeny appears clearly established. I will, therefore, at first very briefly outline an approximate history of land and sea distribution from the late Cretaceous to the present, which affected deployment of faunas, taking into account a large body of literature on plate motion and polar wander (see particularly results of the recent important symposium, Tarling and Runcorn, 1973).

Although a broad, midcontinental sea (reaching from north to south) divided North America in the late Cretaceous, land connection existed between North America and Europe via Greenland and the Barents Shelf until probably the end of the early Eocene (McKenna, 1972). Since the Mesozoic separation of North and South America no land connection was reestablished between these until the end of the Miocene. Final separation of South America and Africa was in the Cretaceous and it appears that the distance between Africa and South America was always greater in the Cenozoic than that between the American plates.

Although the proximity of the African continent to Europe and Asia has not changed substantially during the Cenozoic, the role of the Tethys and Turgai seaways as effective barriers between Africa and Europe and between Europe and Asia, respectively, during the early Tertiary seems well established. The marine environments of the Turgai straits, during the early Cenozoic, and Beringia, intermittently throughout the Cenozoic, acted as filter routes. Sweepstake dispersal between Central and South America, and South America and Africa was possible throughout the Paleogene, although it has clearly become less and less likely during the latter half of the Cenozoic between South America and Africa as these plates have assumed their present positions. The exact geographical and faunal relationships of Africa, Madagascar, and India represent an important and enigmatic problem. During the course of the gradual attainment of their present global positions, sweepstakes dispersal was clearly possible between Africa and Madagascar and Madagascar and India. Just one of the many difficult problems centers on the time of successive positions of the Indian plate prior to its docking to Asia.

As it has been often pointed out in the past,

primate dispersal was greatly influenced by the presence of warm forests with perennial food supply, and therefore indirectly by the climate and, of course, available dispersal routes. Various summary accounts of Tertiary climates based on different approaches agree on a steady if not regular climatic deterioration in the Northern Hemisphere, and some of the causes that effect dispersal and presence or absence of vertebrate species (e.g., such factors as continental positions, orogenies, and subsequent climatic change) were recently reviewed by Walker (1972).

The tarsiiforms were an essentially Holarctic group of primates but their descendants have radiated into the southern continents. Paleozoogeography is intimately interwoven with phylogeny, and discussion of tarsiiform distribution without the remaining primates would be somewhat out of context. In order to place the postulated paleozoogeographic history of the tarsiiforms into perspective, therefore, I will briefly examine the dispersal history of the entire order.

Two of the most recent syntheses of primate paleozoogeography are those of McKenna (1967) and Walker (1972). My interpretation of the evidence for deployment differs from these, partly because I postulate a lesser number of hitherto unknown stocks, but primarily because of my somewhat different understanding of primate phylogeny. Assumptions of phylogeny figured most significantly in interpreting primate dispersal, and this is evident in the syntheses both by McKenna and by Walker, and in my own advanced here. In the discussion to follow, I will invoke the useful model advocated by Kurtén (1967). In essence, this hypothesis suggests that higher categories are probably the result of adaptive radiation of a stock geographically isolated from its closest relatives. Invariably the invasion of the "same" or similar adaptive zone in different areas isolated by barriers, will result in new radiations, depending on space and time.

McKenna held that lemuroids were present only in Africa, whereas his omomyoids (he considered paromomyids also as a primitive family of that group) were present during the Paleocene in North America and, as he suggested, also in Asia. His omomyoids dispersed from Asia to Europe, and the plesiadapids followed the same route. He postulated the spread of lemuroids from Africa to Eurasia and subsequently to North America. Lorisoids were postulated to have evolved from lemuroids in Eurasia during the early medial Eocene. A late Eocene differentiation of pre-catarrhine and pre-platyrrhine stocks in Eurasia and Central America, respectively, is shown by McKenna, prior to the dispersal of these into Africa and South America, respectively.

According to Walker, an ancestral primate stock was present throughout the world (except in Australasia and Antarctica) during the latest Cretaceous to medial Paleocene. Similarly, for the period spanning the late Paleocene to early Eocene this author suggests the presence of lemuroids and omomyids throughout the entire New World and Old World, except for Madagascar, which lacked the omomyids. From the late Eocene to early Oligocene, lemuroids are shown to be present in all places of the previous time period except in South America where they have apparently become extinct. Omomyids at that time were restricted, according to Walker, to both of the Americas and Africa. During late Oligocene to early Miocene, in addition to the actual presence of omomyids in North America, platyrrhines in South America, and catarrhines and lorisoids in Africa, the tarsiids are shown to have been differentiated in Asia and lemurids to be present in Africa. Some of these last assumptions, I believe, unlike some of the previous ones, are well justified.

The following account represents a synthesis of my current views on primate phylogeny fused with available paleogeographical information. A postulated ancestral stock, ancestral to and in general structurally probably very similar to the paromomyiforms of North America and Europe, was widely distributed throughout the northern continents during the late Cretaceous. These mammals, the earliest of which may already qualify to be called primates by basicranial and pedal criteria, were possibly distinct 80-70 million years ago, but the only Cretaceous record so far is the single tooth of *Purgatorius ceratops* (Van Valen and Sloan, 1965). The Paleocene primate fauna of western North America consists of only paromomyiforms, i.e., paromomyids, picrodontids, plesiadapids, and carpolestids. The known Paleocene sites of France and Germany share the

plesiadapines, along with an endemic group of the plesiadapoids represented by *Saxonella.* That paromomyids were also present in Europe is likely as judged by the probably phylogenetic ties of *Berruvius*, a form closely related to the North American *Navajovius.* Absence of picrodontids and carpolestids may indicate that these small forms were endemic to western North America, or simply the poor sampling of European Paleocene faunas may account for their absence.

The evidence from the Eocene primate faunas of western North America and Europe convincingly suggests that the paromomyiforms were superseded by the lemuriforms and tarsiiforms. This is so in spite of the fact that such genera as *Plesiadapis*, *Platychoerops*, *Ignacius*, and *Phenacolemur* linger on. There is no question in my mind that the lemuriform and tarsiiform radiations were already in existence during the Paleocene, but these arenas of evolution are unknown and their locations may only be guessed.

The lemuriform primates, restricted today to Madagascar, were once widely distributed on the Northern Hemisphere. They appear to be widespread during the entire span of the Eocene, with the greatest taxonomic diversity (known so far for that time) apparently in Europe.[1] As I judge from the descriptions and illustrations of the few known tantalizing Asian fossils, they were probably even more varied east of the Turgai Straits in southern Asia. In North America, significantly, there are three known generic groups present: the early Eocene *Pelycodus*, the medial Eocene *Notharctus* and *Smilodectes*, and an undescribed late Eocene genus (Wilson and Szalay, in prep.). *Pelycodus* is also present in Europe, and there, unlike in North America, the adapids are the dominant primates during the Eocene. The lemuriform paleozoogeographic record indicates a Holarctic Eocene distribution, yet the Cretaceous and Paleocene history is so far entirely lacking. Paleocene presence of adapids in Europe or during that time period in the tropical forests of southeastern North America certainly cannot be dismissed. Complete lack of knowledge of the first 20 million years of the Cenozoic of southeast Asia and of the land mammal faunas of the entire Paleocene and Eocene of Africa make speculations difficult. In regard to Africa, the three successive primate faunas of the Oligocene from the Fayum deposits of Egypt with the absence of adapids or noncatarrhine primates in general, might be significant. If one speculates on factors of global tectonics, the possible Asian source for the colonizing tooth-combed lemurs of the Paleocene or Eocene might have been western Asia or the southern part of the continent as it appeared then without the Indian subcontinent. India could have acted as the plate that received northern waifs and was the subsequent source for the colonization of Madagascar, or first the Somali Peninsula and subsequently Madagascar.

The lemuriforms, then, judged by the distribution of the Eocene taxa, may be originally an Asiatic group which gained entry into Europe and eastern North America.[2] Dispersal to Madagascar from Asia or southern Europe probably occurred either in late Paleocene or as late as early Oligocene time, but clearly this question is unsettled. It is quite possible that Africa supported a varied lemuriform fauna during the late Cretaceous, Paleocene, and Eocene.

The lorisiform primates are enigmatic in terms of their place of origin. Either Africa or possibly

[1] It should be added that intra-familial relationship and classification of most adapid genera is difficult to determine because many are known by only a few dentitions, and our knowledge of cranial and postcranial anatomy is poor. Of the Eocene genera, skulls are known only in *Notharctus*, *Smilodectes*, *Pronycticebus*, *Leptadapis*, and *Adapis* and partial skulls in *Protoadapis*. Many new postcranial elements of adapids were recently recognized in several European collections, some of which have been discussed by Decker and Szalay (1973), and others are being studied. Day and Walker (1969) described a humerus from the Hampstead beds (late Eocene or early Oligocene) of the Isle of Wight as belonging to an adapid. Comparisons indicate that the bone probably belonged to a pantolestid insectivoran, member of an extensively aquatically adapted group, several species of which abound in the Hampstead fauna, and not to an adapid.

[2] I should note that northeast Asia cannot be ruled out as a possible source for North American *Pelycodus*. It must be remembered, however, that the early Eocene mammal faunas of Europe and western North America are extremely similar and that a broad land connection forming a corridor was undoubtedly present between the continents during the early Eocene (Savage, 1971; McKenna, 1973).

southern Asia (of the Oligocene) are likely places for the differentiation of the first lorisids from cheirogaleids (see Szalay and Katz, 1973), the latter derived from bona fide lemuroids. I suspect that the lorisids originated either in Africa or Asia from either (a) Malagasy cheirogaleids that reached Africa sometime during the late Oligocene, or (b) endemic members of the Cheirogaleidae, which were originally African, along with possible African lemuroids. At present, I am perhaps more inclined to favor lorisid evolution from Madagascan cheirogaleid waifs reaching Africa, or possibly Asia.

The interpretation of deployment of haplorhine primates is no less problematical than that of strepsirhines. In North America at the beginning of the Eocene an unprecedented radiation of the greatest known bulk of the tarsiiforms, the omomyids, is already under way, whereas, as noted, only one adapid genus, *Pelycodus*, is known there during that time. It is a pure guess that the tarsiiforms may have come north from their more southern and southeastern range of either continental North America or Asia as the climate warmed at the end of the Paleocene. In North America the last remnants of the midcontinental Paleocene Cannonball Sea disappeared at this time. The provenance of *Pelycodus* is likely to be from Europe where the genus is present at this time. Clearly, an Asiatic origin for the genus cannot be ruled out.

The omomyids persist as late as the early Miocene in North America, but their Mesoamerican fate (because there is no record) remains intriguingly unknown. These primitive tarsiiforms might have existed during the Paleocene of North America, perhaps in hitherto unsampled ecological facies of western North America or in the eastern half of this continent or in southern Asia. The North American diversity and abundance could be explained then by either local origins of the tarsiiforms from adapid-like ancestors, probably during the Paleocene in the southeastern part of North America, or by dispersal from Europe, or southern Asia. Deployment, if the origin was Asiatic, was most likely in the form of sweepstakes dispersal across the southern part of the Turgai Straits into Europe and from there to North America. In the case of North American origin, the dispersal would have been in the opposite direction. The European microchoerines are somewhat specialized tarsiiforms that could be descendants of eastern North American or southern European anaptomorphine omomyids. The time of origin for this group may be the same as for the omomyid *Teilhardina* to which the microchoerines may be specially related. Whether tarsiiforms were once diversified in Asia cannot be assessed, in spite of the presence of *Tarsius*, but it seems very likely that the Asiatic land mass, like North America, also contained a large tarsiiform primate fauna during the early and even later Tertiary.

Perhaps as a direct result of the acceptance of a model of a tectonically mobile earth the interesting question of the degree and kind of relationship between platyrrhines and catarrhines and caviomorph and phiomorph rodents was reexamined, mainly by Lavocat in 1969 and Hoffstetter in 1969. They have argued that the platyrrhines of South America are descendants of colonizers arriving from Africa. The geographical origins of hystricomorphous rodents and anthropoid primates are probably tied together, as well argued both by Lavocat (1971) and Hoffstetter (1972). Late Eocene rodents with a clearly hystricognathous lower jaw from the late Eocene of Texas (Wood, 1972, 1973) represent some recently discovered tantalizing evidence. Although both the Anthropoidea and Hystricomorpha are probably monophyletic taxa, the African origin of these categories is not as convincing as Lavocat's and Hoffstetter's arguments suggest (see also Wood, 1973). As I see it, there are two unproved underlying assumptions to their arguments, and there is no evidence that may be unequivocally interpreted to the exclusion of other assessments of the known facts. The assumptions underlying an Africa to South America dispersal hypothesis are (1) that current patterns of the Atlantic facilitated only a western dispersal between those two southern continents, and (2) that Africa received ancestral primate stocks prior to the radiation of the known Oligocene catarrhines.

In light of the widely separated paleopositions of North and South America during the Paleocene and Eocene (see particularly the faunal evidence presented by Simpson, 1948, 1967, and Patterson and Pascual, 1968) the confluent Pa-

cific and Atlantic oceans and other factors, such as the then prevailing wind patterns, may have dictated oceanic currents between the southern continents different from those of today. Thus, the mechanism of dispersal via *existing* currents is questionable. The second assumption, the presence of primates in Africa during the early Tertiary, is clearly unresolved. Admittedly if the introduction of the ancestral anthropoid stock into either South America or Africa is sought, it is perhaps more probable that some haplorhine stock found its way into Africa rather than South America during the late Eocene or early Oligocene as the distance of dispersal from the north was probably less in the case of the former than in the latter. Supposing, however, the sweepstakes dispersal for primates and rodents from southern North America of the late Eocene into South America, the probability, at least as I see it at the present, that their descendants rafted to Africa is not any less likely than westerly dispersal from Africa. For morphological reasons I favor a dispersal hypothesis in an easterly direction. What has actually happened in the course of anthropoid and hystricognath evolutionary history, accepting that these are monophyletic categories, is thus not at all resolved in spite of our knowledge that South America and Africa were substantially closer together during the Eocene than they are today. The evidence of morphocline polarities of features shared by platyrrhines and catarrhines strongly suggests to me a Mesoamerican origin for platyrrhines (and, therefore, a common ancestor for anthropoids) and their dispersal into South America and subsequently into Africa where the Catarrhini evolved from this colonizing stock.

ADAPTATIONS

Perhaps as a direct influence of Cuvier's tradition vertebrate paleontologists have been notorious in making statements on the mode of life of their objects of study. Although they usually lack analyses to support their views, intuitive hypotheses put forward by paleontologists on the "behavior" of fossil taxa should be both welcome and rigorously tested. Why the effort of paleontologists, systematists, functional morphologists, and paleobiologists in general to describe and analyze the morphology of fossil and extant animals? Besides faunal considerations and the attempts to understand the genealogy of animals, the "ultimate" goal is to understand the natural history of a species studied. For living animals this is done through ethological and ecological studies, and the last decade has been the witness to field endeavors of unprecedented zoological sophistication and thoroughness (for some outstanding primate studies see Petter, 1962; Schaller, 1963; Goodall, 1965; A. Jolly, 1966; Hladik and Hladik, 1969; Petter and Peyrieras, 1970; Charles-Dominique, 1971; Charles-Dominique and Hladik, 1971; for an exceptionally fine book on primate natural history, see A. Jolly, 1972).

In order to understand an organism in the most profound way, one should, ideally, first know as much as possible about its behavior and consequently attempt to decipher the morphology and physiology. Clearly paleontologists are at a disadvantage in the study of adaptations. Such study of the fossil mammal record is hampered by a number of formidable factors that may be summarized as follows: (1) Uncertainties whether fossil assemblages of a locality represent a biocenose or thanatocenose; (2) difficulty in assessing the climatic and vegetational characteristics of the environment of deposition; (3) almost total lack of "fossil-behavior"[1]; (4) the usually incomplete record of fossil species; (5) the necessity to reason, largely inductively(?), from the morphological evidence in order to arrive at an estimate of possible behavior and consequently ecology.

Information other than the morphological evidence is rarely more than peripheral to most problems of paleobiology. In fossil assemblages

[1] An outstanding exception known to me: a skull of the fossil Eocene condylarth *Hyopsodus* found in the crop of the giant flightless bird *Diatryma*, obviously eaten by the bird (D. Paris, personal commun.).

with large species counts from the same facies sympatric taxa are clearly differently adapted, and the same applies to the sympatric taxa of a given climatic and vegetational zone of today. Thus, the adaptational profile of a fossil species must be pieced together mostly from the morphological evidence as knowledge of the paleoenvironment is only vaguely helpful.

Whenever complete skulls, dentitions, and skeletons are known (a rare situation, particularly among small vertebrates), analogies with the total morphology of living forms occasionally leads to recognition of approximate ecological vicars of living animals among the extremely well-known fossils. The environment, however, is rarely divided up identically by members of distantly or even closely related radiations. The method of analogy is restricted to a very few species of fossils as it is quite useless for a tremendous number of extinct taxa that probably have no exact or even vaguely similar ecological vicars in the Recent faunas.

A two-level conceptual approach, outlined by Bock and von Wahlert (1965), clearly differentiating between mechanical function and biological role, is perhaps the most helpful one to me for understanding morphology, both of living forms and, in a somewhat modified form, of fossils. These authors define function (1) and biological role (2) as follows: (1) "In any sentence describing a feature of an organism, its functions would be that class of predicates which include all physical and chemical properties arising from its form (i.e., its material composition and arrangement thereof) including all properties arising from increasing levels of organization, provided that these predicates do not mention any reference to the environment of the organism" (p. 274); (2) "In any sentence describing a feature of an organism, the biological roles would be that class of predicates which include all actions or uses of the faculties (the form-function complexes) of the feature by the organism in the course of its life history, provided that these predicates include reference to the environment of the organism" (p. 278).

The phenotype of a species reflects not just the adaptedness to present demands, but is clearly a compromise between the adaptedness of its ancestors and of its own. It is then of obvious importance that to understand adaptations of various species one must have some understanding of the adaptations of the inferred or actual common ancestor. Assessments of the ancestral condition, then, also have great consequences in the evaluation of adaptations in the descendant species.

Finally, inferences on the mode of life of a given fossil taxon must necessarily be based on derived character states. Primitive character states may only represent adaptations of an ancestor, although this does not mean that functions of the primitive morphology and the roles performed by them were not part of the adaptedness of the species analyzed. It does mean, however, that one may only make relatively meaningful statements associated with the role of the derived character-states. The only reasonably certain way of assessing the biological roles associated with the primitive morphology is the occasional *secondary* recurrence of the "primitive" (i.e., advanced when it is secondary) character-states, inferred to function similarly and be adaptive for the same purposes as the *primary* primitive features. This, to repeat, is not meant to imply that primitive characters possessed by any species are not adaptive, or not vitally part of the total adaptive complex of a given species.

An evolutionary trend is understood by me and used in this monograph as being the mode of change in a single lineage, a unilinear character transformation. I do not use the word as it has been often employed in the past to mean a diagnostic combination of ancestral characters to describe or characterize several species, or the independent acquisition of similar, derived character states in a higher category. Thus, there is no "omomyid" trend, but only trends that might characterize particular lineages during a given span of time. As an evolutionary trend is change in an inferred lineage, evolutionary trends are a series of derived character states in any given supraspecific category. These trends are independent of one another; the change may affect homologous characters or entirely unrelated ones in any of the lineages. Needless to say, knowledge of phylogeny must precede inference of trends.

Specific adaptations are discussed under the

Cranium, Dentition, and Postcranial Morphology. The poor cranial material and the lack of associated lower jaws with any of the specimens studied unfortunately do not permit a detailed musculoskeletal analysis of the feeding mechanism.

Under each genus treated in the systematics section I have attempted to outline some fairly broad, general hypotheses, using rudimentary concepts of mechanical function of the known fossils in order to account for the known morphology, usually dental, and consequently postulate their biological role. I am painfully aware of the inadequacy of these accounts yet hopefully they will serve a useful purpose as an initial attempt to interpret, at least in a general way, the feeding mechanism and consequently some aspects of the mode of life of the extinct omomyids.

CRANIUM

The orbits on the tiny skull of *Tetonius* were clearly relatively large, a condition allometrically related to the relatively large brain and small absolute size of this taxon. It is impossible to ascertain whether the relative size of the orbits reflects nocturnal adaptations either in *Tetonius homunculus* or are retentions from a nocturnal ancestor. Judged from the enlarged orbits of *Tetonius* and *Necrolemur* one may suggest that the ancestral omomyid was probably a nocturnal species.

One is struck when studying omomyid maxilla fragments that almost all the taxa known by these parts have a base of the zygoma and an orbital shelf that projects a great deal laterally. Lacking the complete skulls for most of the species it is impossible to relate this to the relatively large size of the eyes, particularly as all the omomyids are small to tiny animals in which one expects relatively large eyes. Marmosets and tamarins, squirrel monkeys, and the talapoin, all diurnal forms, show the laterally projecting orbital shelf. What all these forms, and probably most of the omomyids have in common, although to varying degrees in the omomyids, is well-developed orbital convergence. Thus the well-projecting orbital shelf may not be indicative of relatively enlarged eyes or adaptations to nocturnality, but perhaps represent the well-developed orbital convergence of the omomyid morphotype. Orbital convergence, however, at least in the case of omomyids, might have been an adaptation enhancing visual acuity in a rapidly locomoting ancestor. Whether nocturnality was a factor or not in the development of orbital convergence is a point difficult to argue, but the selective factors brought about by frequent hopping and jumping were likely to have placed great premium on stereoscopy (for different views see Cartmill, 1972).

One of the diagnostic distinctions of haplorhines from strepsirhines, as ascertained above, is the phyletic enlargement of the promontory artery, and I can only offer a speculative hypothesis for this condition. Some selective factors on the earliest haplorhines were perhaps the same as on the earliest cheirogaleids. If the haplorhine morphotype was nocturnal, as was likely the first cheirogaleid, selection would have favored an increase of blood supply to the orbits. Although the pathway of blood-flow through the ear region is different in the two groups, the selective factors responsible for the existence of these divergent, diagnostic characters might have been the same.

It was suggested by Werner (1960) that the failure to enlarge the stapedial artery was due to the limit set on expansion by the stapes. Perhaps this explains why both the haplorhines on the one hand, and the cheirogaleids and lorisids on the other, enlarged and developed another, the promontory, and the ascending pharyngeal arteries, respectively. The enlarged platyrrhine and catarrhine promontory arteries show that the size of this vessel is not limited by the basicranial architecture.

The broken basicranium of *Tetonius* clearly shows signs of an enlarged petromastoid area and a relatively very large middle ear chamber, particularly the hypotympanic sinus, essentially as in *Necrolemur*. Petromastoid inflation is often causally tied to bulla inflation and subsequently to the enlargement of the middle ear cavity. In *Necrolemur*, with an enormous petromastoid, the middle ear cavity, although large, is not as hypertrophied as that of *Tarsius*. Yet in *Tarsius*, which has an enlarged hypotympanic sinus, there is no noticeable petromastoid inflation.

Among living primates the solitary, nocturnal lorisids have a middle ear with multiple partitions and a greatly inflated petromastoid, chambers

which may be open to the middle ear proper. In his remarkably thorough natural history of Gabon lorisiforms Charles-Dominique (1971) noted that galagines feed principally on Orthoptera, Lepidoptera, and small Coleoptera. He stated (p. 224): "Hearing plays a large part in the detection of these insects—many of which are captured in flight by a rapid extension movement in which the Bush-baby maintains a grasp on the branch with its hind limbs. The ears . . . are particularly mobile, permit detection of insects in flight even through an opaque screen." Are some lorisid modifications of the ear structure related to food procuring activities? Petter (1953) has advanced an interesting hypothesis, with some data to support it, on bullar hypertrophy in desert rodents, although it is questionable whether it has much weight in explaining bullar hypertrophy in general or in the primates. He suggested that the greatest bulla hypertrophy is correlated with the lowest population density. Thus, the proportions of the bullae may be viewed as an index of dispersion. Species with hypertrophied bullae usually have a low population density and in a single species the least dense populations would be made up of individuals with the most voluminous bullae. He postulated that the probability of encounter varies inversely with the distance separating individuals. It is stated that the bulla, an acoustic amplifier with its particular qualities, would enhance meetings between the sexes. This hypothesis is interesting and perhaps accounts for bullar hypertrophy of some desert rodents (but see Lay, 1972, and below). The factors affecting either population density or encounter chances may be, of course, not restricted to desert ecologies. Yet bullar hypertrophy in such highly social taxa as *Lemur*, *Indri*, or *Propithecus*, or social carnivores (R. Hunt, personal commun.) would make this hypothesis relatively unlikely. Whatever the specific role of bullar hypertrophy and the possible correlated inflation of the petromastoid to further enlarge the middle ear cavity, the major selective factor was perhaps the improvement of hearing acuity in general. Lay (1972) suggested selection for acuity for a wide range of low frequency sounds in desert rodents, without any selection for particular frequencies in this range. Lay further convincingly hypothesized, at least for desert species, that as the efficiency of carnivores increases with the sparsity of cover where rodents can hide, selection at the same time would operate to increase hearing acuity in the prey and perhaps, I suggest, in the predators also. Thus some form of bullar hypertrophy in the lorisoids, most of which are predatory, and perhaps in some omomyids indicates adaptations to both prey and predator detection.

DENTITION

Mammalian paleontologists rely very heavily on the masticatory system, the teeth in particular, on which they base taxonomic as well as many phylogenetic and evolutionary conclusions. It is of utmost importance, therefore, that this system be understood in the most profound fashion on the level of its mechanical functions and subsequent biological roles. Recently there have been great strides in understanding tooth function (Butler, 1961; Mills, 1966; Crompton and Hiiemae, 1970; Crompton, 1971; Every and Kühne, 1971; Every, 1972; Kay and Hiiemae, 1974). Some advances have been made in determining specific biological roles of some Recent dentitions in relation to diet (Ride, 1959; Seligsohn and Szalay, In press; Walker and Murray, In press). The greatest stumbling block in the way of further knowledge is exact, comparative accounts of feeding regimes of closely related species of mammals. To understand dental morphology of past species one should go beyond comparative systematic accounts on which phylogenies are based, to determine function and postulate hypotheses of dietary or other habits. Studies in which attempts are made to establish causal relations between teeth, their function, and the animal's diet are in their infancy (but see Seligsohn and Szalay, In Press; and Walker and Murray, In Press). Many such studies on mammals are needed before their results can be employed meaningfully in the study of ancient radiations. Until this new science of morphology becomes better founded, remarks on inferred adaptations of omomyids or other fossil mammals should be regarded as suggestions or crude hypotheses that cannot be tested because we have not accumulated knowledge on living forms as yet.

In general, the most important finding of numerous field studies of primates has been that sympatric species consistently follow their own

dietary regime, subdividing the food resources in a species specific manner. Although far from being proof, this suggests that specific selective forces act on the feeding mechanism and this, in turn, suggests that taxon specific adaptations are causally correlated with feeding adaptations.

As a rule, the biological role of dentitions is usually determined by vague morphological comparisons with dentitions of living species with a known diet. This method can be extremely deceptive when only molars are utilized, as some poorly known fossil taxa, which share many primitive molar similarities with living ones, are often interpreted to have had similar food preferences to the living analogues. Minor morphological changes and noticeable body size changes in the living forms from ancestral patterns that might signify major adaptive shifts are thus often overlooked and no causal explanations, but rather merely badly understood correlations, tie the morphology of the crown pattern of living species to this diet. Although still based on analogy, comparison of complete dentitions, area by area, tooth by tooth, has been more reliable in assessing possible broad feeding preferences of fossil species.

The most thorough and sophisticated surveys of primate diets in the wild (in particular Hladik and Hladik, 1969; Petter and Peyrieras, 1970; and Charles-Dominique, 1971) reveal both species specific and habitual dietary regimes, particularly in rain-forest environments in which niche width is probably relatively narrow. The supplied dietary profiles, vigorously researched and analyzed by Hladik and Hladik (1969) and Hladik et al. (1971) on several species of platyrrhines clearly show, that, as stated by Hladik and Hladik (1969, p. 115), "Each species of primate has a specific dietary regime. Each has its own particular preferences. These preferences are not simply 'opportunistic' responses to the food available. Different species feed on different things in the same areas." Charles-Dominique (1971, p. 225), in his study of Gabon lorisoids, pointed out that even in the tropical ecosystem, "There is a critical period (dry seasons) during which the availability of food (insects, fruits) reaches a minimum. With some of the prosimian species (for which there is adequate sampling throughout the year), it has been shown that there is a reduction in ingested food and loss in body weight in individual animals during this critical period. Examination of the digestive tract shows that dietary specializations are far more distinct during the peak of the dry season than at any other time during the year. Thus, during the critical period, *E. elegantulus* eats gums and no fruit, whilst *P. potto* eats no gums, whereas these two species will eat both fruit and gums for the rest of the year." I have surveyed the dental morphology of primate species on which field studies have been conducted and concluded that by a method of analogy comparing the whole dentition of fossil forms to those of living species it is possible to suggest, at least as a hypothesis to be eventually tested by empirical methods, one of five broad diet categories for fossil taxa. The categories may be called, from one extreme to the other, folivorous, frugivorous, omnivorous, gumivorous, and insectivorous-carnivorous (see also A. Jolly, 1972). The two extremes, folivory and insectivorous-carnivorous specializations, are probably recognized with a high degree of probability. Frugivorous and omnivorous feeding regimes, on the other hand, are less well-defined categories because most species considered frugivorous consume a fair amount of leaves and insects to satisfy protein and lipid requirements.

In many groups of mammals in which dentitions have not been excessively modified, the differences between closely related taxa are subtle. Consequently interpretation of functional (mechanical) significance as they relate to their biological roles requires a combination of field studies of eco-ethology and a scrutiny of morphology. Clearly, functional studies of fossil taxa are even more uncertain. Yet, as understanding of the close causal relationships between dentitions, their individual elements, and their biological roles in living taxa becomes more comprehensive, questions asked of fossils will become increasingly sophisticated.[1]

[1] One of the best places to start to understand biological meaning in mammalian dentitions should be the relatively easily accessible, small, and most primitive and ecologically diverse therians. Thus, to understand the dental and eventually feeding adaptations of early Tertiary mammals the ecology, feeding habits in particular, of the small metatherians of South America, Australia, and New Guinea and most of the small Carnivora and Insectivora will need extensive investigations. Scrutiny of the diversified dental adaptations and natural diet of these groups will supply immense amounts of information and the necessary models to understand different kinds of dentitions not excessively specialized from a tribosphenic ancestry.

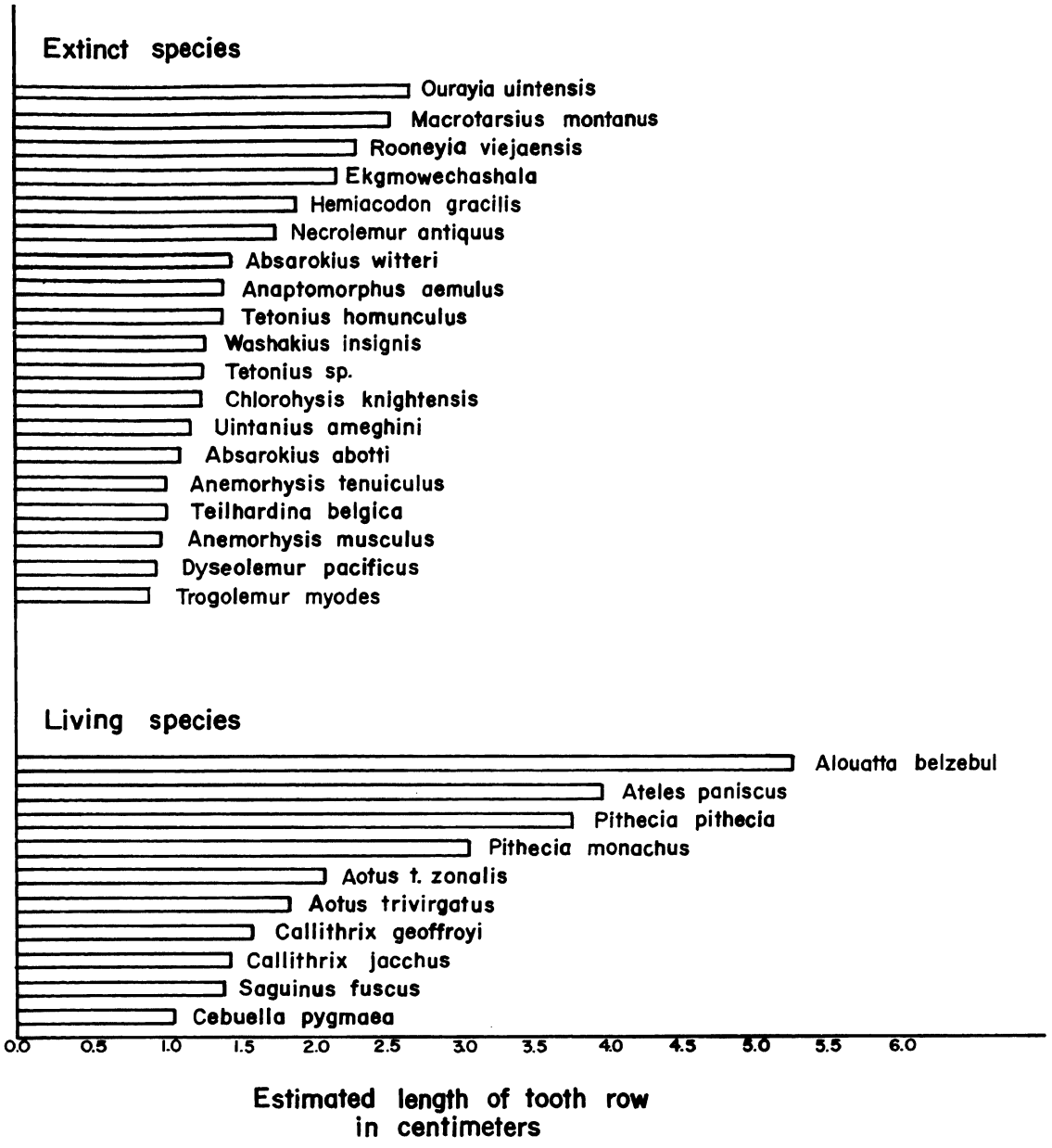


FIG. 177. Estimated length of the tooth row of some omomyid species compared with some living platyrrhines to give a measure of relative size of the extinct taxa.

I would like to discuss briefly some points pertaining to specific areas of dentitions and some related problems. In general the anterior part of the dentition (incisors and canines) is most instrumental in the manipulation of food objects. Manipulation means activities ranging from cropping, gnawing, cutting, grasping, and piercing a variety of vegetable matter, to catching, holding, or piercing prey species.

In general the cheek teeth behind the canine are usually used for the actual trituration of the food secured by the anterior dentition or hands.

It is well known that the premolars, in addition to their holding function, may also be used to hone the upper canine, as in catarrhines (P_3).

A number of features can be listed that may be significant when assessing divergence in terms of mechanical properties of occluding antecanine and cheek teeth in closely related species: (1) relative size of the teeth to each other, (2) relative height, length, and breadth of the tooth, (3) nature of cutting edges and apices or their absence on the crown, (4) relative length and alignment of cutting edges exposed, (5) relative thickness of enamel (the degree of furrowing and enamel papillation is probably also related to the amount and kind of edges available for cutting), (6) characteristic food-caused wear patterns on the crown, (7) direction of occlusal movements as inferable from crown morphology, and, to some degree, cineradiographic studies, (8) characteristic wear or perhaps thegosis (either alpha or beta kind, see Every, 1972), (9) specific edges of the crown worn or thegosed more than others, and (10) relative robusticity and, in general, the morphology of roots.

The unique and very often socially utilized tooth comb of living strepsirhines is discussed here, as the problems in their interpretation illustrate some methodological procedures of morphological inference. This highly modified region of the dentition (except in *Daubentonia madagascarensis*) offers an excellent opportunity both to test and illustrate the importance of adaptations of the ancestral condition and their influence on the descendants' morphology, as well as the power of resolution of a mechanical analysis in order to relate mechanical function to biological role. It also enables the student to see the arrangement of morphocline polarity of some very subtly differentiated character states of a relatively well-delineated character complex.

I believe that the lemuriform and lorisiform anterior dental specializations are shared derived characters and not convergent, a conclusion which follows from the analysis of the phylogeny of living strepsirhines (see under Phylogeny and Classification) and one which leads to the following question: What were the selective factors responsible for the evolution of the tooth comb among strepsirhines? To answer this requires a somewhat complex analysis. A mere correlation of the tooth combs with their use without the mechanical analysis can be very misleading, particularly when the anterior dentition is used in a variety of ways by closely related living species. Martin (1972, p. 331) has presented a discussion of this very same question. His conclusions, largely deductive, are summed up by him (p. 329): "There is no doubt that the tooth-scraper is used by many (if not all) lemurs and lorises for grooming; but this is probably a secondary function. Field observations have shown that the smaller-bodied Cheirogaleinae and Galaginae use the tooth-scraper to gather plant exudates, and it is likely that the horizontal arrangement of these anterior teeth has been primarily developed for scraping and prising. A. F. Richard (personal commun.) has observed *Propithecus verreauxi* feeding extensively on bark, using prising actions of the modified tooth-scraper. Since the lower canines have (remarkably) undergone complete modification, a novel combination of selection pressures must be invoked to explain this as an early development in the ancestral lemur/loris stock:

"(1) The early development of manual mobility in Primates alleviated the grasping functions of the anterior dentition (transfer of prehensile function from the snout to the hands).

"(2) The partial switch to plant food reduced dependence upon trapping small animal prey with the anterior dentition.

"(3) The radiation of the vascular plants provided new opportunities for sap-eating in addition to fruit- and leaf-eating. Licking of plant exudates could have preceded adaptations for scraping.

"(4) Small-bodied mammals would have been less dependent upon canine teeth for defense against predators, relying instead upon rapid escape.

"Given these factors, it is conceivable that the scraping function of the anterior teeth was more important for sap-eating species than the stabbing, prehensile function of the lower canine. Nevertheless, it is obvious that functional modification of the canine was only possible under exceptional conditions, since in many of the larger lemurs there has been secondary modification of the first lower premolar as a caniniform tooth."

As I disagree with both Martin's method of analysis and his conclusions, I will reexamine this relevant problem. Since a morphological analysis is not presented, I conclude that the nature of functional inferences used by Martin are heavily influenced by his inferred phylogeny of living strepsirhines. This has resulted in Martin's seeming conviction that the use of the tooth comb in the ancestral strepsirhine mode of life was more like that in galagos and some cheirogaleids than in the more diurnal, larger, more gregarious taxa of lemurids.

The tooth combs of strepsirhines are well known, yet a number of attributes should be highlighted because a combination of these have not received recognition or attention by workers studying them. The curious fact that the canine joins the incisor area and takes up the derived form of the incisors is significant in two respects. First, it is probably not selection for a long mesial cutting edge which prompted this event. Increasing the alleged mesial cutting edge of the anterior teeth by adding another pointed, narrow tooth to that area of the dentition creates a discontinuous edge which has neither the cutting ability of a continuous one nor the strength or penetrating ability of a pointed, and mesiobucally robust tooth. Second, the canine joining the incisors in the front results in a very significant feature, the creation of an additional, long, narrow interdental space. The same clearly applies to the modifications of the whole tooth comb; all six front teeth have five narrow, evenly distributed spaces between them in the primitive strepsirhine tooth comb. Unlike in incisors among most primates the apical extremities of the anterior teeth are not any nearer to one another than the basal portions.

Thus, I conclude that the primitive strepsirhine tooth comb is primarily adapted for the efficient maintenance of optimally long, parallel, narrow spaces rather than resistance of stresses incurred by the apices of the teeth in cutting or scraping. The biological role, which would explain this ancestral morphology, appears to be the fur-combing function, originally attributed to this specialization, during which forces are not excessive and are distributed more or less evenly on the long and narrow occlusal surfaces of the anterior teeth.

A self-evident but important fact should be added here: among the living primates it is the strepsirhines who possess a tooth comb, and these primates are also the ones that use it as a comb for the explicit purpose of grooming. Aside from the mechanical function of the tooth comb, the suggestion from mere correlation is very strong that this derived anterior dental structure, along with additional modifications of the tongue in the form of the sublingua (Jones, 1929), is the direct result of selection to fulfill the biological role of fur cleansing.

The pivotal argument to explain the morphology of the tooth comb for sap eating should come from an analysis of the most highly adapted sap eaters *Phaner* and *Allocebus* (Petter, Schilling, and Pariente, 1971) in contrast to their closest relatives *Cheirogaleus* and *Microcebus.* Yet, it is *Phaner* that excessively (for Malagasy strepsirhines) enlarges the central upper incisors in a manner opposite to those found in other forms, displays robust canines, adds another caniniform tooth, the premolar, to the upper dental battery, and clearly extremely reduces the relative post-caniniform surface area of the cheek teeth. Notably, the tooth comb is relatively longer and the lower canines are more robust than those in other lemuriforms. From a mechanical point of view it appears that all these conditions, which are derived, came about to serve as tools that can withstand the great shearing stresses incurred during nipping and tearing of bark and they mirror the decreased necessity of the cheek teeth for trituration of a food which is usually very soft. The African *Euoticus* shows the same adaptations of the anterior dentition as does *Phaner.*

Living lemuriforms also offer us the example of *Daubentonia madagascariensis* in which the morphology of the mesiodistally very wide and buccolingually narrow, ever-growing, heavily worn incisors offer the best conceivable mechanical solution for chisel-like penetration by the leading edges that run largely buccolingually, and maximum stress resistance is in the direction of both orthal and propalinal jaw movements. In the aye-aye the temporomandibular joint well reflects the direction and extent of the habitual movements of the jaw in an anteroposterior direction. The biological role of the incisors are

well known in the aye-aye; they are the main tool of this lemur to gnaw into the cambium and woody tissues of trees bearing larvae of wood-boring insects. Convergence by the living marsupials *Dactylopsila palpator* and *Dactylonax trivirgata* strongly supports the causal relationship between the mechanical function and biological role of the teeth.

Tarsius exhibits an anterior dentition, along with the premolars, in which the very pointed single cusped morphology of the teeth and their occlusal relations point to the maximizing of orthal piercing and penetration. The biological function of this anterior dentition, as can be inferred from both laboratory and field accounts, lies in its use as a combination killing and holding device. The prey caught by the hands and feet is killed and probably segmented into smaller pieces by the anterior dentition with the help of the hand.

The little that is known of omomyid anterior dentitions is discussed under the respective genera. These adaptations are tantalizing for they allow a glimpse into an adaptive divergence of the anterior dentition which was undoubtedly extensive. Adaptations of omomyid cheek teeth are not stereotyped either, but rather very diverse. Even within the same subfamily there appear to be specializations of whole dentitions that may reflect mechanical solutions from extremes of herbivorous feeding (e.g., *Washakius*) to extremes of catching and masticating insects and small vertebrate prey (e.g., *Chumashius*). Although the morphology of the molar dentitions (except for *Ekgmowechashala*) is not extremely divergent, the dental differences noted among the taxa warrant the numerous inferences advanced under the respective genera concerning their biological role. In order to show some aspects of the structure and presumably functional diversity of omomyid dentitions I have prepared simple indices of the relative functional areas of the cheek teeth from P_3-M_3 (the usual lack of fossils prevented the coverage of the anterior dentition) in some of the better known species (table 29). Relating the loosely termed functional area of an upper or lower tooth (the product of length and width) to the sum of the functional areas of the teeth from the third premolar to the last molar, either above or below, allowed a visually striking comparison (fig. 178). The qualitative details, and their possible reflection of specific biological roles, discussed under the respective genera, clearly underline the great diversity of omomyid feeding adaptations.

The use of either dental proportions (relative functional area patterns, a term coined by Katharine Milton, personal commun.) or the mechanical analysis of individual elements of the dentition must be firmly grounded on the best possible assessment of the morphotype for a given taxon. What ideally matters is the evaluation of qualitative change, the adaptive shift, in the teeth from inferred common ancestors to descendants in a monophyletic taxon rather than the differences among many species of varying recency of relationships of a higher category. The gist of this type of comparison is that adaptations reflect divergence of one form from another, the ancestor, or between two or more closely related taxa from a common ancestor, and these inferable differences should be analyzed for mechanical and biological meaning.

Regardless of the morphology inherited once a lineage has made an adjustment to procurement and processing of its species specific food resources, dentition proportions, coupled with careful qualitative evaluation of crown patterns, may be effective in predicting broad feeding patterns. Difficulty in prediction must lie with those taxa which just diverged from the ancestral taxon of an adaptive radiation. They carry with them the attributes of the ancestor yet, as several taxa have diverged and have come to exist sympatrically, these descendant species may show only the rudiments of adaptive responses for the particular new way of life which is divergent from the ancestral one. Antiquity of certain food preferences is as difficult to judge in living taxa as in fossil ones, yet both the relative antiquity of occupancy and, probably more so, the intensity of selective forces must be reflected in the degree of adaptations for a particular feeding regime (but see some relevant discussions by Eldredge and Gould, 1972).

Our ability to interpret symphyseal remains is in its infancy, in spite of the fact that often well-

TABLE 29

Dental Modules $\left(m = \frac{xA}{\Sigma xA}\right)$ of Some Omomyid Primates[a]

(The estimated functional "area" of a crown is simply the product of the greatest width and length of the tooth.)

Taxon	mP_3	mP_4	mM_1	mM_2	mM_3	mP^3	mP^4	mM^1	mM^2	mM^3
Tetonius homunculus	.13	.19	.25	.23	.19	.19	.22	.24	.24	.10
Anemorhysis spp. (3 species)	.11	.18	.24	.23	.24	.17	.19	.23	.25	.15
Absarokius abotti	.15	.23	.23	.23	.16	.20	.25	.23	.23	.09
Omomys carteri	.14	.17	.23	.23	.23	.14	.16	.24	.25	.20
Loveina zephyri	.14	.18	.25	.22	.20	–	–	–	–	–
Hemiacodon gracilis	.13	.15	.24	.24	.23	–	–	–	–	–
Ourayia uintensis	.12	.14	.24	.24	.26	.12	.14	.24	.27	.22
Washakius insignis	.11	.15	.21	.22	.30	.15	.18	.20	.25	.22
Shoshonius cooperi	–	–	–	–	–	.15	.17	.22	.25	.20
Uintanius ameghini	.18	.34	.18	.16	.14	.22	.22	.21	.21	.13
Chumashius balchi	.16	.19	.23	.22	.19	–	–	–	–	–
Dyseolemur pacificus	.11	.15	.22	.25	.26	–	–	–	–	–
Ekgmowechashala philotau	.11	.21	.28	.22	.18	–	–	–	–	–
Teilhardina belgica	.12	.17	.25	.27	.18	.14	.20	.25	.26	.14

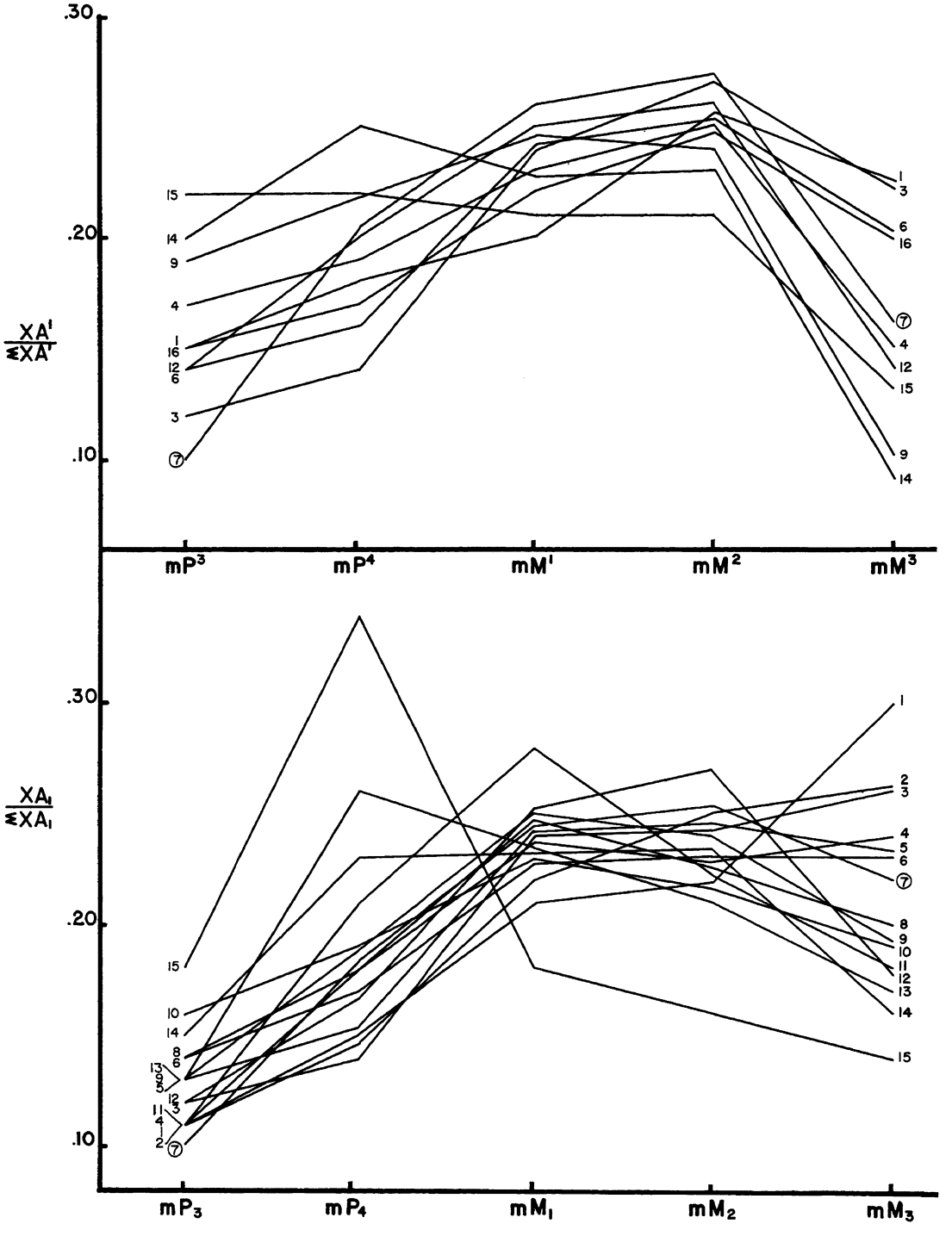
[a]See also figure 178.

preserved symphyses are the only available information in addition to a fragmentary mandible for many genera of mammals. I do not know of any tarsiiform genus which has a fused symphysis. Nevertheless the causes of certain symphyseal configurations can be explained essentially by the same selective events which result in symphyseal synostosis. This phenomenon is perhaps best explained as the necessary result of most effectively engaging the contralateral musculature in the functions of the actively chewing, ipsilateral side. Thus, although in a synostosed symphysis the stresses are actually greater than in a mobile one because the forces cannot be dissipated at the symphysis, the increase in stress is the indirect result of selection to increase the force and efficiency of some aspects, usually the mesiolingual component, of the masticatory stroke of the cheek teeth.

POSTCRANIAL MORPHOLOGY

I have elsewhere, along with others (Decker and Szalay, 1973; Szalay and Decker, 1973; Szalay, Tattersall, and Decker, 1975) begun a series of studies on early Tertiary primate postcranials. Separate studies on the postcranial adaptations of various Tertiary primates are under way in which many undescribed omomyid specimens are being treated in detail along with those presented in this monograph. A few remarks on omomyid postcranial adaptations are, however, pertinent at this point. Much of the discussion set forth under Phylogeny and Classification is clearly relevant to this section.

In small mammal quarries of the North American Eocene there is a local abundance of flattened, undoubtedly nail-bearing terminal phalanges that probably belonged to omomyids. These specimens are too small to have belonged to either *Notharctus* or *Smilodectes* species, but are in the size range expected for *Omomys*, *Hemiacodon*, and *Washakius* of these localities. Presence of these nails as opposed to claws in omomyids is highly suggestive of the mode of life of these primates. Claws are of undoubted advantage to an arboreal animal that habitually moves up and down and around on large branches and tree trunks. In contrast to the advantages of nails for posturing and secure moving around on relatively broad, steeply inclined surfaces, flattened nails are ideal when thin branches have to be grasped. Thus, a mode of life in which grasping


.30
.20
.10
XA'/ΣXA'
mP3
mP4
mM1
mM2
mM3
.30
.20
.10
XA1/ΣXA1
mP3
mP4
mM1
mM2
mM3

hands and feet are needed, such as foraging in terminal branches (Cartmill, 1972), would favor the flattened, small nails. As the cheiridia grasp and wrap around a thin branch, claws should not obstruct the efficiency of the encircling fingers or cause injury to the hand itself.

On the first metatarsal of *Hemiacodon* (AMNH 12613, fig. 171) the area of attachment for the peroneus longus is enormous compared either with homologues on known adapids or the living strepsirhines. As it is known only in *Hemiacodon* this keel-shaped process cannot be said to be representative of the omomyids in general. For that genus, however, it suggests that unusually great forces, probably associated with grasping, were incurred at this area.

The advanced nail-bearing as opposed to clawed cheiridia and powerful grasping feet of at least some omomyids would indicate terminal branch milieu ecology at least for the common ancestor with nails. Presence of nails clearly cannot be used beyond this rudimentary explanation as the ancestral nature of this feature does not necessarily set limits on its use for purposes other than that for which it originally evolved.

The differences between the biological role of a form-function complex in a given species, e.g., the tarsus of *Microcebus murinus* and the cause of its evolution in the lineage leading to that species, should be recognized. The subsequent selective factors operating on a form-function complex are often different from those initially implementing its evolution, as repeatedly stressed above. Thus, not all of the known omomyids with an elongated calcaneum were necessarily foot runners on delicate limbs, jumpers, leapers, or vertical clingers and leapers, although the primitive condition in the family, i.e., the elongated calcaneum, was probably derived for the role of improving some such actions. The numerous derived lineages that retained the ancestral form were not necessarily habitual practitioners of the ancestral locomotor pattern!

Some of the omomyid, as well as adapid, postcranial evidence figured prominently in the hypothesis of Napier and Walker (1967a, 1967b) that the common ancestor of known strepsirhine and haplorhine primates was a vertical clinger and leaper. Some views on their analyses have been published by Cartmill (1972), Szalay (1972b), and Decker and Szalay (1973). Stern and Oxnard (1973) presented a critical review of the reported locomotions of strepsirhines and *Tarsius*, and a few of their morphological correlates without discussing any of the joints. Their assessment is built around an all-pervasive premise that the morphology studied in a given species is a reflection of characters acquired during the existence of that species as we know it, for locomotor behavior as we now recognize it. The numerous methods they suggested for the study of morphology, most helpful in taxonomic discrimination, appear to me to sidestep phylogenetic aspects of form and mechanical function. In using such analyses, although they may satisfy demands for a purely quantitative science, one cannot hope to understand morphology without primarily understanding joints and an equally im-

FIG. 178. Relative functional areas of omomyid check teeth (P_3-M_3). Dental modules (m) represent mean "area" (xA) of the tooth (the product of the greatest mean buccolingual width and greatest mean mesiodistal length) divided by the sum of the mean individual dental areas for that species (ΣxA). The resulting graphs show the estimated relative importance of a given tooth within the tooth row of that taxon. This data is incomplete partly because of lack of good samples and partly because of the absence of the anterior part of the dentition in the fossils. The functional importance of crown height and the extremely important qualitative differences of crowns are not reflected. Only when qualitative characters of the crowns and the relative size of the animal are considered can the relative functional areas be fully appreciated. Thus, for *Uintanius ameghini* (15), for example, mP^3 and mP^4 do not adaquately demonstrate the extremely divergent nature of these premolars. The numbers represent the following species: 1) *Washakius insignis*; 2) *Dyseolemur pacificus*; 3) *Ourayia uintensis*; 4) *Anemorphysis* sp.; 5) *Hemiacodon gracilis*; 6) *Omomys carteri*; 7) *Palaechthon alticuspis*, a paromomyid included for comparison; 8) *Loveina zephyri*; 9) *Tetonius homunculus*; 10) *Chumashius balchi*; 11) *Ekgmowechashala philotau*; 12) *Teilhardina belgica*; 13) *Absarokius noctivagus*; 14) *Absarokius abotti*; 15) *Uintanius ameghini*; 16) *Shoshonius cooperi*.

portant phylogenetic analysis of the total evidence. Without clear ordering of morphocline polarity and the assessments of morphotypes for taxa compared, and without hypotheses that envisage morphological stages in the studied lineages, evolutionary morphology cannot be meaningfully practiced.

In their analysis of the Mahalanobis-generalized distances for scapular measurements of a large number of primate species, Stern and Oxnard stated that (p. 22), "although *Galago* and *Propithecus* are outlying to the main mass of forms [i.e., of the running-leaping-quadrupedal primates], they do not exhibit any special relationships to one another, being on opposite sides of the central group." As a possible explanation they suggest (p. 22), "that there may be, morphologically at least, more than one kind of vertical clinging and leaping." The differences in the anagenetic history in the two groups is perhaps purposefully sidestepped, but the point is made, namely that biological history as a source of explanation for differences in biological features is not necessary to consider.

Stern and Oxnard (1973, p. 34) posed direct questions about the locomotor mode, rather than about mechanical function, of the Eocene primate remains, reviewed the literature on the reported fossils, and commented in detail mostly on aspects of the specimens discernible from the illustrations published. They stated (p. 38) in a carefully measured manner that, "vertical clinging of a type could have been an important locomotor behavior of primates ancestral to the Anthropoidea, without invoking the image of a tarsier or sifaka for the ancestral forms," a conclusion I am inclined to agree to but with some important refinements. The possibility that the Eocene adapid morphotype, a form distinctly more primitive than a haplorhine morphotype, was a vertical clinger and leaper is unlikely (see analysis presented in Decker and Szalay, 1973). This, therefore, makes the inference that the common ancestor of nonparomomyiform primates was a vertical clinger and leaper (as advocated by Napier and Walker, 1967a, 1967b) also unlikely. Skeletal adaptations of known omomyids, however, although still poorly understood in the joint morphology, an area of greater importance for assessing habitual posturing than limb proportions, do indicate features that may be correlated with rapid locomotion, and, at least in *Hemiacodon*, possible vertical posturing. Thus, a clear indication that the omomyid morphotype was an agile and rapid runner and perhaps a habitual leaper is very strong. To my knowledge, however, no known data suggest the mechanical functions required for vertical clinging and leaping in the anthropoid morphotype.

Stern and Oxnard noted that (pp. 31, 34): "These various findings from both pelvic and shoulder girdles, from both hind and forelimbs, all suggest that there is more than one kind of morphology among 'vertical clingers' and, therefore, that there is likely to be more than one kind of vertical clinging and leaping . . . This information is derived from a number of quite separate and independent investigations. Because it is so marked, it strongly suggests that even if the behavioral information that is currently available pointed to a single category of vertical clinging and leaping, we should be searching diligently for indications of behavioral differences among the many species." I suspect that whatever minor differences may be discovered in the future in the manner in which vertical clinging and leaping is executed, they will not adequately explain the many distinctive differences in bone and joint morphology of such phyletically widely separated, but similar sized, taxa as, for example, *Tarsius* and *Avahi*.[1]

[1] Contrary to the prevalent, somewhat nonphylogenetic, approach to the explanation of species-specific bone morphology appropriate questions posed to the distinctive phyletic histories of the lineages will eventually be necessary to clarify the meaning of divergences and convergences. In my view, useful as the available technological expertise is for taxonomy and for some morphological studies, syntheses of problems in evolutionary morphology will require the asking of proper morphology related questions and gathering of answers pertaining to unique phylogenetic histories. Despite technological advances which led to the collection of new kinds of data and particular kinds of data analyses, and which supply powerful tools for morphological discrimination (see important review by Oxnard, 1972), the conceptual methods of phylogenetic (e.g., Hennig, 1965) and comparative morphological inference (e.g., Bock and von Wahlert, 1965) will be major determinants of a modern comparative method of evolutionary morphology. The novel approaches to data gathering and clustering afforded by the computer explosion (as those reviewed by Oxnard, 1972) and morphological analysis utilizing quantitative techniques (e.g., Bock, 1966; Preuschoft, 1970, 1971) are most significant for understanding correlations between related aspects of form or the physics of morphology in terms of the forces acting on them.

THE TARSIIFORM ANCESTOR

If one considers the overall general similarities of most known fossil tarsiiforms (inasmuch as they were small arboreal species) to present-day tarsiers, small platyrrhines (particularly callithricids), cheirogaleids, and galagos, and is fully aware of the specifics of phyletic relationships as discussed above, the general analogy that these fossils were not unlike the groups listed is a broadly valid one (see also Cartmill, 1972). An attempt to answer some of the more refined questions, for example, whether the ancestral tarsiiform (probably an omomyid) was diurnal or nocturnal, insectivorous or frugivorous, social to what degree (this is clearly tied to the first two questions), and what was the characteristic posturing and locomotion of this ancestor, is perhaps beyond the power of resolution of this study or maybe of the available evidence. It seems reasonable to conclude, however, judged by the structural diversity displayed by the known omomyid fossils (assuming greater intrafamilial differences in the postcranial morphology than that known at present), that the tarsiiform radiation of the early Tertiary produced species probably as diversified in their mode of life as are all present-day primates in their size range.

I quote Gregory's (1951, p. 470) view of the primitive tarsiiform specializations: "The advanced specializations of the early tarsioids for arboreal nocturnal habits, reduction of the olfactory sense, great enlargement of eyes, increasing ability to make huge leaps and grasp the tree in landing, all placed the premium of survival upon a rapidly increasing brain; this in turn may have been the focal point of selection in the post-tarsioid stages that are preserved in the New World monkeys." We now recognize that such an assessment of the primitive specializations perhaps unduly relies on the still poorly known mode of life of *Tarsius*, although it may still have merit. Many unexplained facts remain even in relation to the only living tarsiiform. *Tarsius* lacks a tapetum behind its retina and perhaps the extreme enlargement of its eyes is partly the result of this condition. If one suggests that the tarsiiform morphotype was nocturnal, it is difficult not to suggest that it has probably evolved a tapetum, and in that case one would be forced to state that *Tarsius* is a descendant of an advanced, diurnal tarsiiform which has lost its tapetum. This question is clearly unresolved both for the ancestral tarsiiform or for species of *Tarsius*.

It is perhaps true that modern tarsiers which are predatory, occasionally terrestrial, crepuscular-nocturnal, silent, and not very gregarious primates (Fogden, 1974) are not likely to very closely resemble the tarsiiform or omomyid common ancestor. Nevertheless, an element of nocturnality along with insectivory appear to be likely behavioral components in the repertoire of the ancestral tarsiiforms.

Judged only from the generally small size of omomyids, their ancestor was also a very small form, and perhaps more insectivorous or omnivorous than the putative immediate ancestry for the better known adapines. As I have argued above on the subject of the enlargement of the promontory artery, this shift may have been a selective response to increase blood supply to the brain and perhaps also to the eyes either to supply an enlarged eyeball in an ancestral species, nocturnal or predatory or probably both.

I cannot help noticing a very close parallel between the origin of the first tarsiiform from a primitive strepsirhine stock and the differentiation of the first cheirogaleid from lemurids, probably under very similar selection pressures during different geological times and geographical settings.

SUMMARY

The Omomyidae of the early Tertiary is arranged to contain four groups of subfamily rank: the Anaptomorphinae, Omomyinae, Ekgmowechashalinae, new, and Microchoerinae. As a result of the revision of the first three subfamilies the combined number of known species included in these three groups is 34, and the number of genera in which they are arranged is 24. The Microchoerinae, not revised here, are known by approximately eight additional species, arranged in four genera. One new species and genus, the Wasatchian *Mckennamorphus despairensis*, and a new species, the Bridgerian *Anaptomorphus westi*, of omomyids are described.

In assessing the genealogy of taxa within the Omomyidae the most diverse and abundant evidence, the dentition, was primarily utilized. The following new categories, in addition to the Ekgmowechashalinae, new subfamily, were used to arrange a balanced classification of the Omomyidae: Trogolemurini, new tribe, Washakiini, new tribe, Uintaniini, new tribe, Utahiini, new tribe, and Rooneyiini, new tribe. The newly described genus *Donrussellia*, based on a known species, from the Sparnacian of France cannot be allocated with certainty to the Omomyidae; this form may have closer ties and more recent affinities with primitive Adapidae, although the relevance of this genus to the stem Omomyidae is emphasized. The classification of the Omomyidae was constructed to reflect the adaptive divergence displayed in the known anatomy as well as to be consistent with the phylogeny inferred. The taxonomic history, phylogenetic ties, and some inferred adaptations of all these genera are discussed under Taxonomy, Phylogeny and Classification, and Adaptations.

Judgments on the relationships of the family to other primates were based largely on basicranial and postcranial morphology, as well as on dental evidence. Both the morphotypes of the basicranial organization and known postcranial remains of the Omomyidae point to an ancestral condition easily derivable from some primitive adapid primates. The omomyid character states of several known features are invariably derived compared with the more primitive conditions of the adapid morphotype. The postcranium and the cranium of the Adapidae and Omomyidae, however, have numerous shared and derived character states that attest to the monophyly of the ancestral families of the Strepsirhini and Haplorhini. A derivation from a species that would be considered as adapid based on cranial, dental, and postcranial evidence is postulated for the Omomyidae.

In examining the relationships within the Tarsiiformes, it is concluded that the most primitive group of this category is probably the Omomyidae, as exemplified by the Anaptomorphinae and Omomyinae. Specializations found in the basicranial morphology and dentitions of the Microchoerinae on the one hand and the Tarsiidae on the other are not shared between these two groups. Tibiofibular fusion of the Microchoerinae may not be a unique character of the subfamily but rather a characteristic of the Omomyidae. Possession of divergent specializations and sharing of only possibly primitive tarsiiform characters between the Microchoerinae and Tarsiidae strongly argue against special relationships and hence against the inclusion of the former group within the Tarsiidae. The specialized condition of the basicranium and the numerous unique, advanced soft anatomical attributes shared between the Tarsiiformes, Platyrrhini, and Catarrhini warrant the monophyletic status of the suborder Haplorhini in which these categories are included as infraorders. The monophyly of the Anthropoidea seems well established in light of the shared and derived characters unique to anthropoids but not found in known tarsiiforms.

An inferred dispersal history for the primates is presented. As far as the meager fossil evidence suggests, paromomyiform primates were not present in South America and Africa during the Cretaceous and Paleocene, whereas on the northern continents they were well established during the early Tertiary. The main arena of strepsirhine evolution appears to have been Europe and Asia although presence of varied stocks of African strepsirhines prior to the Miocene cannot be

ruled out. Dispersal of the original stock of tooth-combed lemurs to Madagascar or Africa was probably from Europe or Asia. Although the descendants of primitive haplorhines, the platyrrhines and catarrhines, have dispersed to the southern continents, the known record indicates the Tarsiiformes to have been a Holarctic group. The origin of the Anthropoidea is probably from southern North American tarsiiforms, and the direction of dispersal was to South America and subsequently across the Atlantic to Africa at low northern latitudes. Dispersal in the opposite direction cannot be ruled out, and in that case origin of the anthropoids was more likely from Asiatic or southern European tarsiiforms.

Some of the known adaptations of fossil tarsiiforms and some pertinent strepsirhines are discussed and an attempt is made to envisage aspects of behavior and ecology of the ancestral tarsiiform. This species was probably a nocturnal insectivore. The enlarged promontory artery of the tarsiiform ancestor, as the anterior carotid artery of the nocturnal cheirogaleid lorisoid, was probably a means of increasing the blood supply to the brain for various functions perhaps related to predation. These adaptations were accompanied by the apparent increase in sophistication of running and saltatory locomotion as suggested by the postcranium. The rapid locomotion of the ancestral tarsiiform probably supplied powerful selective forces for augmenting the centers in the brain responsible for an increase in visual and auditory memory and a more efficient processing and integration of visual and auditory stimuli. These conclusions are specific for the earliest tarsiiform adaptation and do not appear to apply to the Adapidae, and therefore to primitive strepsirhines in general.

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